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LIST OF PAPERS

I. New Merycodonts from the Upper Miocene of Nevada. By Eustace L. Furlong. Pages 1 to 10 and 5 plates.

II. Two Rodents and a Lagomorph from the Sespe of the Las Posas Hills, California. By Robert W. Wilson. Pages 11 to 17, 1 plate and 1 text-figure.

III. A New Species of Dipoides from the Pliocene of Eastern Oregon. By Robert W. Wilson. Pages 19 to 28, 1 plate and 1 text-figure.

IV. Plants in the Dung of Nothrotherium from Gypsum Cave, Nevada. By J. D. Laudermilk and Philip A. Munz. Pages 29 to 37 and 11 plates.

V. Tooth Characters of Protohippine Horses with Special Reference to Species from the Merychippus Zone, California. By Francis D. Bode. Pages 39 to 63, 2 plates and 6 text-figures.

VI. The Fauna of the Merychippus Zone, North Coalinga District, California. By Francis D. Bode. Pages 65 to 96, 2 plates and 10 text-figures.

VII. A Miocene Mammalian Fauna from Sucker Creek, Southeastern Oregon. By David W. Scharf. Pages 97 to 118, 2 plates and 11 text-figures.

VIII. Artiodactyla from the Sespe of the Las Posas Hills, California. By Chester Stock. Pages 119 to 125 and 1 plate.

CONTRIBUTIONS TO PALÆONTOLOGY

I

NEW MERYCODONTS FROM THE UPPER MIOCENE OF NEVADA

By Eustace L. Furlong

With five plates

[Issued May 25, 1934]

CONTENTS

Page
Introduction 3
Occurrence 3
Preservation and Description of Material 4
    Merycodus loxocerus n. sp 4
    Merycodus hookwayi n. sp. 6
Correlation of Parts 7
Distribution 8
Conclusions 10

NEW MERYCODONTS FROM THE UPPER MIOCENE OF NEVADA

INTRODUCTION

In an Upper Miocene assemblage of mammals recently brought together, occur remains of numerous individuals referable to the genus *Merycodus*. The collection represents several seasons of palæontological field work by parties from the California Institute of Technology in the vicinity of Tonopah, Nevada.

The specimens of *Merycodus* exhibit characters that are not common to those of species described from other localities in the Great Basin Province or from West Coast Miocene and Pliocene deposits. In some respects, the new Nevada forms combine characters seen in *M. furcatus* and *M. necatus*, found in deposits of similar age. Differences of structure among the materials represented indicate the presence of two distinct species of Tonopah merycodonts.

In a study of the new types, an analysis of the morphologic characters of the genus emphasizes the essentially constant premolar tooth pattern for *Merycodus*. As may be expected, greater diversity occurs among merycodont horn-core structures, particularly as to shape and size. However, the supraorbital position of the horn-cores is apparently constant within specific groups.

In the present comparative studies, I am particularly indebted to Dr. Charles L. Camp and to Mr. R. A. Stirton of the Museum of Palæontology, University of California, for the loan of *Merycodus* material. Mr. John L. Ridgway has prepared the drawings and has arranged the plates.

OCCURRENCE

Remains of *Merycodus* from near Tonopah were found associated with *Merychippus*, *Hypohippus*, Rhinoceros, Camel, *Pseudælurus* and other Miocene mammals at California Institute Technology Locality 172. The bone bed occurred in a relatively restricted area in the San Antonio Mountains and in strata referred to Esmeralda Miocene.

The matrix surrounding the bone is a fine clay to a coarse, pebbly sandstone and occasionally a siliceous chert. Some of the fossil bones were imbedded in part in the softer matrix and in part in the indurated chert. Lenses of the latter in the deposit suggest that deposition occurred in a small lake or in ponds.

PRESERVATION AND DESCRIPTION OF MATERIAL

No complete skulls or mandibles of *Merycodus* were recovered, and relatively few limb elements were likewise found. A number of maxillaries and numerous rami with teeth occur. Fortunately, series of complete superior and inferior dentitions illustrate early stages of wear of deciduous teeth to advanced wear of permanent teeth with all intervening changes of crown pattern.

For the large number of individuals represented by rami, horn-cores and frontlets, there is a notable lack of axial and appendicular parts. In fact, the latter comprise only the distal end of a humerus; a hind leg lacking the femur; distal ends of three tibia; one complete and two proximal halves of metatarsals; parts of three calcani; a navicular-cuboid and a number of astragali and phalanges. In contrast, no less than sixty individuals are represented by rami, maxillaries, horn-cores and frontlets.

The frontlets with horn-cores and the detached horn-cores show diversity in size and form. Some of the differences are probably due to individual variation, age and sex. Pathogenic characters likewise may be exhibited. Certain constant characters which are present, when taken in association with dental structures, definitely exclude the Tonopah forms from specific identity with *Merycodus osborni*, *M. necatus*, *M. furcatus*, or with other known types.

A study of the cranial, dental and skeletal parts naturally segregates the collection into a large and a small group. The large group represents a species which may be described as follows:

Merycodus loxocerus n. sp.

Type specimen—No. 1301 C. I. T. Coll. Vert. Pale., right ramus.

Paratypes—No. 1268, left maxilla; Nos. 1298, 1256 and 719, rami, No. 1271, maxillary; and Nos. 696, 697, 698, 702, 705, and 707, horn-cores.

Merycodus loxocerus is characterized by the backward inclination of the horn-cores at an acute angle; lower molar teeth with sharply ridged anterior and posterior crescents; frequent occurrence of intercrescentic columnettes in $M\overline{1}$ and $M\overline{2}$, and by constancy in length of inferior dental series.

Merycodus loxocerus is represented in various stages of development from early youth to advanced age by the horn-cores and tooth series. The horn cores rise from the supra-orbital surface of the frontals, but do not possess the erect position seen in *M. necatus* and *M. furcatus*. In their position with relation to the orbit and in backward inclination, the horn-cores approximate more closely those in *M. osborni*.[1] They differ from those in *M. osborni* in having a practically straight beam and in possessing invariably two tines. Specimen No. 698 (Plate 1, figs. 2 and 2a) is an example of a young adult with slender beam, short anterior tine and relatively long posterior tine. Certain differences in proportion, due to individual variation or to age, occur in specimens No. 705 (Plate 2, figs. 1 and 1a) and No. 696 (Plate 3, figs. 1 and 1a). The former is not so slender and its front tine is less developed, while in specimen 696 the tines are more fully grown, also their curvature toward the sagittal line is more pronounced. These specimens all possess burrs that occupy positions a short distance above the base of the beam. Specimen 697 (Plate 2, figs. 2 and 2a) is somewhat abnormal in growth and is probably a young individual in which the front tines have been suppressed. Many other specimens show incipiency of growth of anterior tines. All of the foregoing specimens probably represent young forms, and a cross-section of the proximal part of their beams is quite circular and the surface of the horn-cores is not deeply grooved by nutrient canals.

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[1] W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 20, art. 7, 101–129, 1904.

Specimens that are considered as belonging to adults of advanced age are notably more robust, although the beam and tines are relatively long. Specimens Nos. 702 to 707 (Plate 4, figs. 1, 1a and 2) and No. 1447 (Plate 1, figs. 1 and 1a) illustrate the larger size, deeper grooving of the horn-core surfaces and more oval cross-section through the beam. In the larger and older individuals, the proximal end of the beam is quite triangular in cross-section with apex forward.

The frontlets show the horn-cores to be parallel with one another and not widely spaced and that they arise from the posterior portion of the supraorbital rim. The orbits are relatively large but not so prominent as in *M. osborni.* A most constant character in *Merycodus loxocerus* is the long slender beam with relatively short tines. *M. furcatus*[1] is distinguished by a like character, when compared with *M. necatus,* but the beams are not so slender relative to their height as in *Merycodus loxocerus.*

The uniformity of character in the large series of horn-cores, which range in size from small immature specimens to large apparently adult forms from Locality 172, indicates considerable specific stability in this respect.

Dentition—Merycodus loxocerus is represented by a large number of lower jaws, a right fragmental ramus, and full cheek-tooth dentition of a young adult, No. 1301. The crown pattern in the premolar and molar series is close to that in *M. necatus* and in other species of *Merycodus.* Premolar teeth with slightly worn crowns have the transverse crests and general pattern essentially similar in P$\overline{2}$ to P$\overline{4}$ inclusive.

The molar teeth in general are typical of the Antilocapridæ, but the crescentic pillars are more sharply ridged than in *M. necatus* or in *M. furcatus* (Plate 4, figs. 4 and 4a). Many of the specimens, as in No. 1301 (Plate 2, figs. 4, 4a and 4b) possess inter-crescentic columnettes in M$\overline{1}$ and M$\overline{2}$, and in the numerous paratypes this character is fairly constant. A comparable style between the anterior crescents of M$\overline{2}$ (Plate 2, figs. 4, 4a and 4b) may be present in a number of specimens. The third lobe in M$\overline{3}$ differs from that in *M. necatus,* U. C. No. 26781 (Plate 3, figs. 5, 5a and 5b), in being more lobate, not angular, and laterally compressed. In *M. furcatus,* U. C. No. 26795 (Plate 4, figs. 4, 4a and 4b), this character is more sharply emphasized. The lower dental series is fairly constant in anteroposterior diameter, with a maximum length of 46.8 mm. in an old adult specimen, No. 1259.

A left fragmentary maxillary, No. 1268 (Plate 2, figs. 3 and 3a) and No. 1267, a specimen with unworn teeth (Plate 3, figs. 3 and 3a), preserve the outer wall and retain the teeth P$\underline{3}$ to M$\underline{3}$ inclusive. The teeth do not differ significantly from those in *M. necatus* or in other *Merycodus* species. In another specimen, No. 1271 (Plate 1, figs. 3 and 3a), right P$\underline{2}$ is present and a complete tooth series is thus available. The buccal side of the alveolar wall develops an irregular surface, caused by prominence of the anterior roots of the cheek-teeth, a character not observed in *M. necatus* or in *M. furcatus.*

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[1] E. L. Furlong, Univ. Calif. Publ. Bull. Geol., vol. 17, No. 4, 1927.

It is possibly an age character, for in another specimen, No. 1264, in which the complete deciduous dentition is present, the prominence of root wall is apparent only in the region of Dp $\underline{2}$ and Dp $\underline{4}$. The crown of M$\underline{3}$ is just appearing above the alveolar border in this specimen.

In adult individuals the tooth-row closely approximates 42.0 mm. in anteroposterior diameter (table 1).

Limb Elements—A hind leg lacking the femur (Plate 4, figs. 5, 5a, 5b and 5c), No. 1446, is referred to *Merycodus loxocerus.* Its slender proportions probably indicate a young adult individual.

The tibia, No. 1446, is long (Plate 4, fig. 5a); its proximal third is somewhat crushed, but the cnemial crest is high and the articular facets for the femur normal. The distal articular end is narrow with a high malleolar facet for the fibula and deep articular facets for the astragalus. In structure and proportion, the tarsal bones and phalanges are much like those in *M. necatus* and in *M. furcatus.*

Merycodus hookwayi n. sp.

Type specimen—No. 1257 C. I. T. Coll. Vert. Pale., ramus.

Paratypes—No. 710, maxillary; No. 712, ramus, and No. 1240, frontlet.

All specimens are from C. I. T. Locality 172.

Merycodus hookwayi is characterized by horn-cores much heavier than in *Merycodus loxocerus* or in *M. furcatus.* Their attitude, in relation to the orbit, is not so erect as in *M. necatus* or in *M. furcatus,* but the posterior inclination is less than in *Merycodus loxocerus.*

The inferior teeth are large with higher crowns, and the premolars are more simple in pattern than in *M. necatus* or in *Merycodus loxocerus.*

A frontlet with horn-cores, No. 1240 (Plate 5, figs. 1 and 1a), appears to present an anomalous type among the merycodonts from Locality 172. It is much heavier than the slender horn-cores described above. In comparison to the latter, this specimen is relatively broader across the frontals, as measured between the horn-cores. The beam is short and the tines likewise are relatively short. The posterior tine curves backward and toward the sagittal line. The horn-cores are more erect in attitude above the orbital rim than in *Merycodus loxocerus,* although inclined slightly posteriorly. Anteroposteriorly, in the region of bifurcation, the core is very broad. A large burr encircles the beam a short distance above its base.

Dentition—The following described jaws and teeth, differing as they do from those of *Merycodus loxocerus* in greater size and small numerical representation, are tentatively considered as representing the same type of merycodont known by the frontlet, No. 1240.

A right ramus, No. 1257 (Plate 5, figs. 3, 3a and 3b), is broken away at both ends; the tooth-row is complete with the exception of M$\overline{1}$; the ventral margin is present and shows decided convexity of surface from the posterior end of M$\overline{3}$ to the anterior end of P$\overline{2}$. The teeth indicate slight wear and are high crowned. P$\overline{2}$, P$\overline{3}$ and P$\overline{4}$ are characterized by high median transverse crests. The anterior crest in P$\overline{2}$ is low. Posteriorly, the crown is divided into two transverse crests. In P$\overline{3}$ the anterior crest is higher than in P$\overline{2}$, and in the latter a slight indentation is represented which becomes a deep infold in P$\overline{3}$, making the two transverse crests forward of the median apex. The back of the crown is divided into two transverse ridges, a deep pit separating the two. The enamel infolds from the lingual side in P$\overline{2}$ and P$\overline{3}$ are deep and extend beyond the fore and aft median line of the teeth, reaching downward to the cingulum.

The anterior crest in $P\overline{4}$ is not transverse in position, and terminates in a shallow notch on the lingual wall. A small lake lies anterior to the median crest, a character absent in *M. loxocerus.* In the latter species, however, a deep infold is present on the lingual wall of the tooth. The lingual wall in side view is like the anterior wall in the molar teeth; the anterior crest forming an anterior style. The median crest equals the anterior crest in molar teeth and is separated from the posterior part of the tooth by a deep infold of enamel.

The back of the crown is divided by a deep pit, with walls converging rapidly to the bottom, and with no infold on the inner side of the tooth. The posterior face of the tooth is slightly convex dorsoventrally. $M\overline{1}$ is absent in No. 1257. $M\overline{2}$ has anterior and posterior crescents sharply ridged from alveolus to crown. The anterior and posterior crests are flanked by a front and back style. $M\overline{3}$ has anterior crescents like the crescents in $M\overline{2}$. The anterior crest possesses two cuspules on its outer crown surface; the front style is strongly developed. The third lobe is not expanded and has a flat plane, posterior face. There are no intercrescentic cusps in $M\overline{2}$ or $M\overline{3}$. $M\overline{3}$ approximates in size and form the third molar of *M. altidens*[1] from the Upper Snake Creek beds. It differs in being smaller and more expanded anteroposteriorly; the anterior lobe of the tooth is relatively longer than the middle and posterior lobes, while in *M. altidens* the anterior lobe is relatively shorter.

The greatest diameter, $P\overline{2}$ to $M\overline{3}$ inclusive, is 56.3 mm. (table 1).

Superior dentition—Specimen No. 710 (Plate 5, figs. 2 and 2a), referred to *Merycodus hookwayi,* represents a fragmental left maxillary which includes part of the buccal wall and $P\underline{2}$ to $M\underline{2}$ inclusive. The teeth are those of an adult and show considerable wear. $P\underline{2}$, $P\underline{3}$ and $P\underline{4}$ differ little in detail from comparable teeth in other merycodonts, and this is true also for $M\underline{1}$ and $M\underline{2}$. The tooth-row is not so sinuous as in *M. necatus* or *M. furcatus,* but is straighter in its longitudinal alignment. The outer side of the maxillary is peculiar in the prominent expansion of surface covering the front roots of the cheek-teeth, thus leaving a depressed area between the front roots of the teeth at the alveolar border. Length of the dentition is approximately 51.2 mm. (table 1).

CORRELATION OF PARTS

Only a relatively small number of lower jaws and maxillaries can be definitely associated, due to the widely scattered distribution of the merycodont remains in the deposits. All of the frontlets and horn-cores were found separate from other cranial or facial parts. Segregation of the materials into two groups seems to answer best the representation of the merycodonts in the Tonopah fauna.

The largest assemblage of material representing *Merycodus loxocerus* considerably exceeds in number of specimens the collection on which is based the species *Merycodus hookwayi.* In the former group, individuals differing in age from youth to advanced adults are represented by specimens with deciduous to much worn permanent teeth. A representation of age characters is expressed also in stages of development of the horn-cores.

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[1] W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 50, art. 11, 198–206, 1924.

Merycodus hookwayi, known by remains of possibly more than three individuals, is distinct from *Merycodus loxocerus* in dental characters and in horn-core proportions. While the parts of the dentition and the horn-cores were not found associated, each individual specimen differs so widely in structural characters from its counterpart among specimens grouped under *M. loxocerus* as to suggest rather strongly that all relate to a single type, distinct from the latter.

With the exception of two relatively large astragali and a calcaneal fragment, possibly referable to *Merycodus hookwayi*, the limb elements in the collection are regarded as belonging to *Merycodus loxocerus*.

Among the horn-cores and frontlets known from the Tonopah locality, specimen No. 1240 (Plate 5, figs. 1 and 1a) is unique in its robustness and in the attitude of beam with reference to the skull, as well as in position of the tines. It is possible, owing to the similarity of dental characters among merycodont species, that certain specimens now grouped under *Merycodus loxocerus* actually belong to the former type.

An analysis of the measurements given in table 1 indicates a close uniformity of size for the tooth-row and for individual teeth among specimens referred to *Merycodus loxocerus*. The specimens measured are all adult forms, but the stage of wear represents individuals ranging in age from very mature to younger adult forms. The differences within the group are not very large. The limited material available of the species *M. necatus* and *M. furcatus*, in each instance representing an individual of well-advanced age, is intermediate in size between that of *Merycodus loxocerus* and that of *Merycodus hookwayi*.

DISTRIBUTION

Species of *Merycodus* form an integral part of the later Miocene and early Pliocene faunas from western North America and are known to have ranged during these stages of the Tertiary from the western Great Plains to and beyond the Great Basin Province.

M. necatus and *M. furcatus* with their variants are among the more commonly recognized forms. These are the species found in faunas of the Barstow Miocene, Ricardo Pliocene, Republican River Lower Pliocene, and Snake Creek Upper Miocene.

M. osborni[1] is apparently a more restricted species from the Pawnee Creek middle Miocene beds of Colorado. This species differs considerably from *M. necatus* and *M. furcatus* and approaches *Merycodus loxocerus* in position of the horn-cores and apparently also in size.

The upper Miocene merycodonts from near Tonopah may have been derived from a stock closely allied to *M. osborni* and may have occupied a similar life-zone, although of somewhat later age.

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[1] W. D. Matthew, Amer. Mus. Nat. Hist., vol. 20, art. 7, 101–129, 1904.

TABLE 1—*Measurements (in millimeters)*

	Merycodus loxocerus n. sp.											*Merycodus hookwayi* n. sp.	
	No. 713	No. 717	No. 1247	No. 1248	No. 1249	No. 1250	No. 1252	No. 1259	No. 1261	No. 1298	No. 1307	No. 712	No. 1257
$P\bar{2}$ to $M\bar{3}$, inclusive, long diameter	44.0	43.0	45.4	45.3	......	......	45.2	46.8	44.0	45.4	44.8	59.6	56.8
$P\bar{2}$, long diameter	4.5	......	......	4.4	5.0	......	......	4.9	4.8	......	4.8	....	6.0
$P\bar{3}$, long diameter	5.2	6.6	5.7	6.3	6.3	5.8	6.6	6.1	6.4	6.0	6.0	....	6.9
$P\bar{4}$, long diameter	6.6	6.7	6.6	6.6	7.0	7.5	5.7	7.3	7.2	6.9	6.9	*a*7.8	8.9
$M\bar{1}$, long diameter	6.9	7.0	7.5	7.6	7.8	7.0	7.8	8.1	7.7	7.2	7.4	9.2	....
$M\bar{2}$, long diameter	7.8	7.7	8.4	8.2	9.0	8.2	8.0	9.4	8.1	8.0	8.3	10.4	11.0
$M\bar{3}$, long diameter	12.5	12.6	12.8	12.0	......	11.1	12.0	12.3	11.5	12.0	11.8	15.0	14.0

	Merycodus loxocerus n. sp.		*Merycodus hookwayi* n. sp. No. 710		*M. necatus* U. C. No. 26781	*M. furcatus* U. C. No. 26745
	No. 1266	No. 1271				
$P\underline{2}$ to $M\underline{3}$, inclusive, long diameter	41.8	40.2	*a*51.0	$P\bar{2}$ to $M\bar{3}$, inclusive, long diameter	51.4	50.7
$P\underline{2}$, long diameter	6.4	6.0	7.4	$P\bar{2}$, long diameter	5.5	4.9
$P\underline{3}$, long diameter	....	....	7.4	$P\bar{3}$, long diameter	5.9	5.4
$P\underline{4}$, long diameter	6.1	....	6.8	$P\bar{4}$, long diameter	6.6	6.8
$M\underline{1}$, long diameter	7.2	6.6	8.5	$M\bar{1}$, long diameter	7.6	8.3
$M\underline{2}$, long diameter	8.2	8.3	10.0	$M\bar{2}$, long diameter	8.8	10.0
$M\underline{3}$, long diameter	8.4	8.8	....	$M\bar{3}$, long diameter	16.0	15.2

a, approximate.

CONCLUSIONS

New species of *Merycodus*, not heretofore reported, occur in beds of the Esmeralda formation of upper Miocene age near Tonopah, Nevada. *Merycodus loxocerus* is represented by many individuals and is associated with the more sparsely occurring species, *Merycodus hookwayi*. Remains of both forms and of associated mammalian types were uncovered in a relatively small area, where they had evidently accumulated in a small lake or watering hole.

Merycodus loxocerus exhibits considerable uniformity of tooth structure and of the structure of the horn-cores in the large series of specimens available. This species approximates *M. osborni* more closely than it does other known species in pattern of the teeth and in the position of the horn-cores.

If the lower jaw specimens, Nos. 1257, 712, pertain to the same species as the frontlet, No. 1240, the species *Merycodus hookwayi*, established on the basis of frontlet as type, may be distinguished from *M. loxocerus* not only in shape and proportions of horn-cores, but also by its marked difference in size and in pattern of the premolar teeth. The higher crowned teeth and peculiar enamel pattern of $P\overline{4}$ in *M. hookwayi* may warrant a generic recognition of this form, when more material becomes available.

PLATE 1

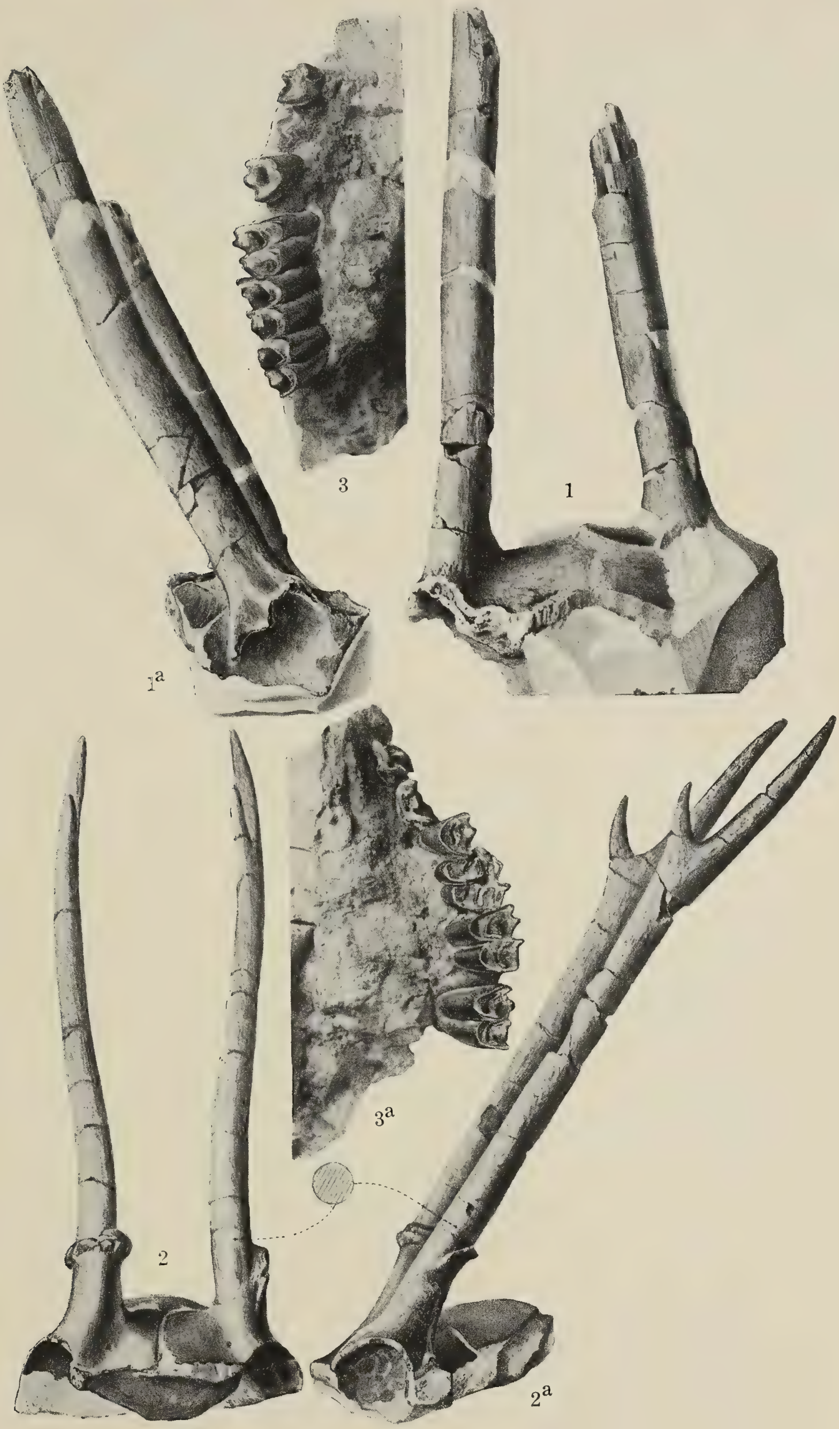
Merycodus loxocerus n. sp.

FIG. 1—Front view of frontlet of mature individual; 1a, lateral view; No. 1447; x ½.

FIG. 2—Front view of frontlet showing closely spaced and parallel position of horn-cores; figure 2a, lateral view showing long beam, relatively short tines and sharp postorbital inclination of horn-cores; No. 698; x ½.

FIG. 3—Right superior dentition; figure 3a, left superior dentition; No. 1271; x 1.

Calif. Inst. Tech. Coll. Upper Miocene, Tonopah, Nevada.



Merycodus loxocerus n. sp.

PLATE 2

Merycodus loxocerus n. sp.

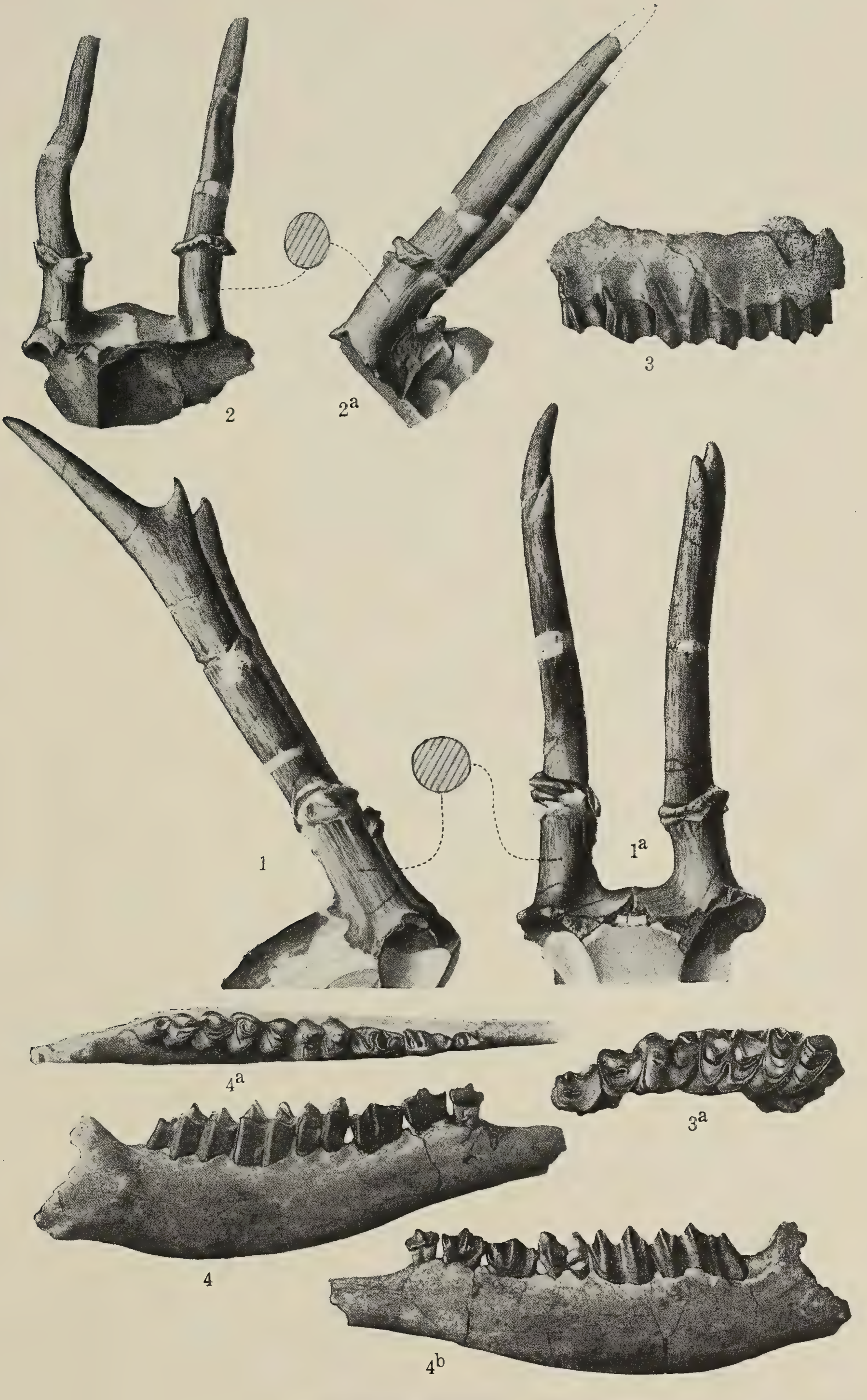
FIG. 1—Side view of frontlet; figure 1a, anterior view; No. 705; x ½.

FIG. 2—Front view of frontlet; figure 2a, side view showing abnormal growth of horn-cores in young individual; No. 697; x ½.

FIG. 3—Side view of left maxillary with depressed areas in wall between roots of cheek-teeth; figure 3a, occlusal view; No. 1268; x 1.

FIG. 4—Buccal view of left ramus illustrating sharp crescentic pillars, intercrescentic columnettes; figure 4a, occlusal view showing transverse crests in premolars and lobate form in posterior crescent of M3; figure 4b, lingual aspect of ramus showing deep infolds in walls of premolars; No. 1301; x 1.

Calif. Inst. Tech. Coll. Upper Miocene, Tonopah, Nevada.



Merycodus loxocerus n. sp.

PLATE 3

Merycodus loxocerus n. sp.

FIGS. 1, 1a—Front and lateral views of frontlet with horn-cores; No. 696; x ½.

FIG. 2—Fragment of right horn-core showing superficial character of burr; No. 687; x ½.

FIGS. 3, 3a—Lateral and occlusal views of maxillary with slightly worn P3 to M3; No. 1267; x 1.

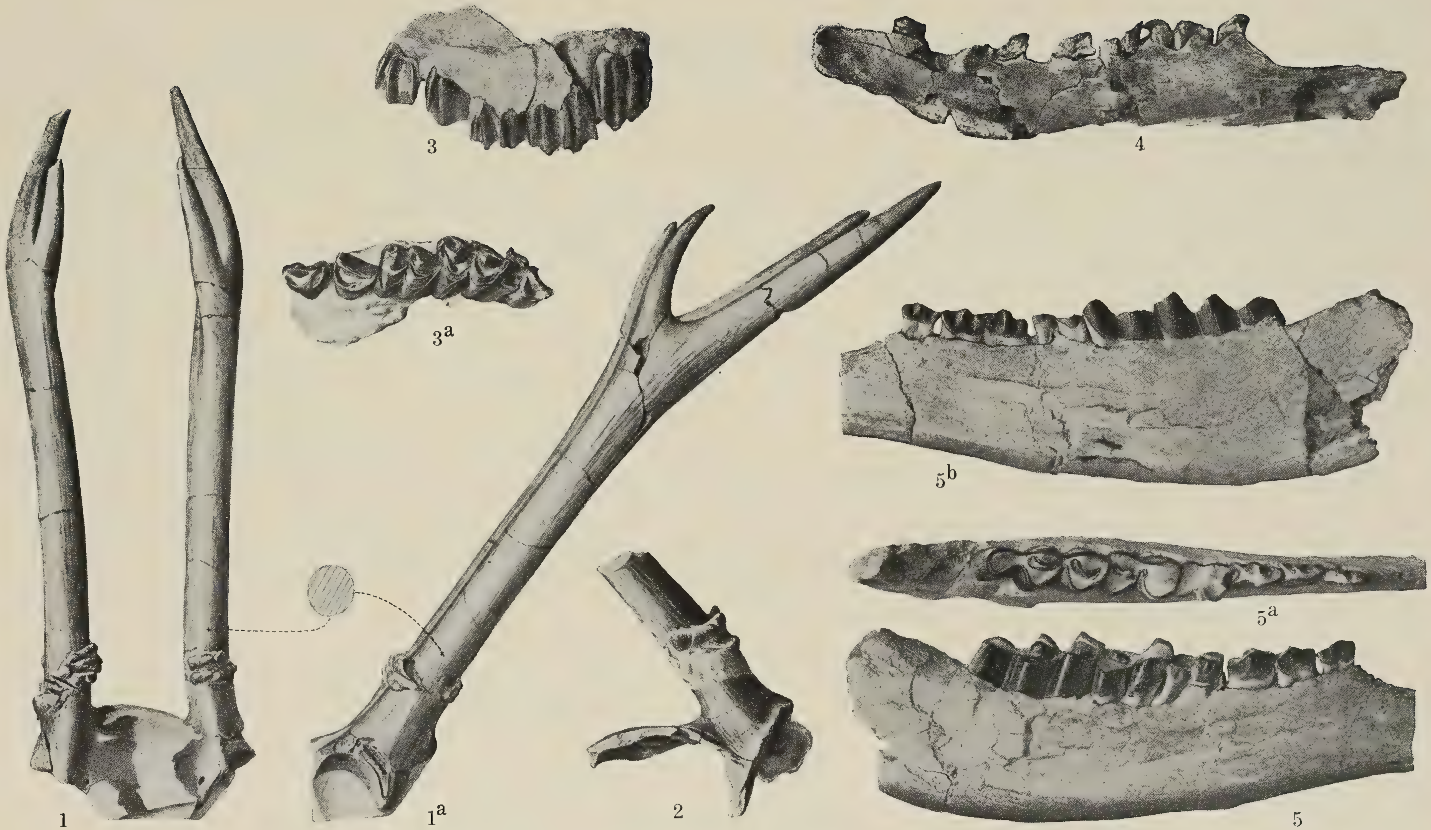
FIG. 4—Lingual view of ramus of an old individual; No. 1256; x 1.

Calif. Inst. Tech. Coll. Upper Miocene, Tonopah, Nevada.

Merycodus necatus Leidy

FIGS. 5, 5a, 5b—Views of ramus to compare with specimen of *Merycodus loxocerus* shown on Plate 2, figures 4, 4a, and 4b; No. 26781; x 1.

Univ. Calif. Coll. Barstow Miocene, California.



Merycodus loxocerus n. sp. and *Merycodus necatus* Leidy

PLATE 4

Merycodus loxocerus n. sp.

FIGS. 1, 1a—Horn-cores of adult individual showing long beam, deep sinuses, and oval cross-sections; No. 707; x ½.

FIG. 2—Distal portion of horn-core; No. 702; x ½.

FIG. 3—Buccal view of right ramus; No. 1298; x 1.

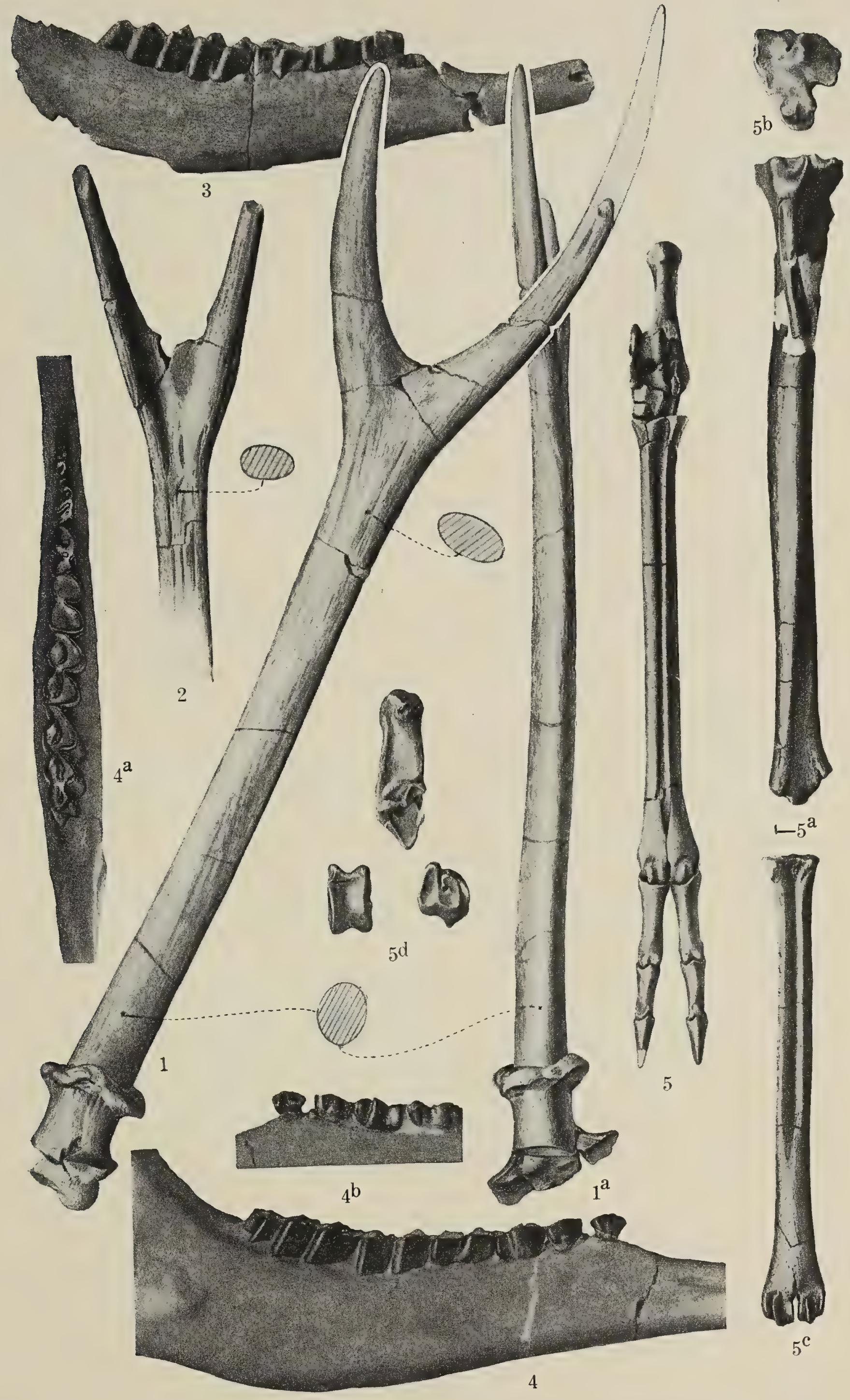
FIGS. 5 to 5c—Elements of the hind leg; No. 1446; x 1.

Calif. Inst. Tech. Coll. Upper Miocene, Tonopah, Nevada.

Merycodus furcatus Leidy

FIGS. 4, 4a and 4b—Views of ramus and inferior dentition; No. 26795; x 1.

Univ. Calif. Coll. Ricardo Pliocene, California.



Merycodus loxocerus n. sp. and *Merycodus furcatus* Leidy

PLATE 5

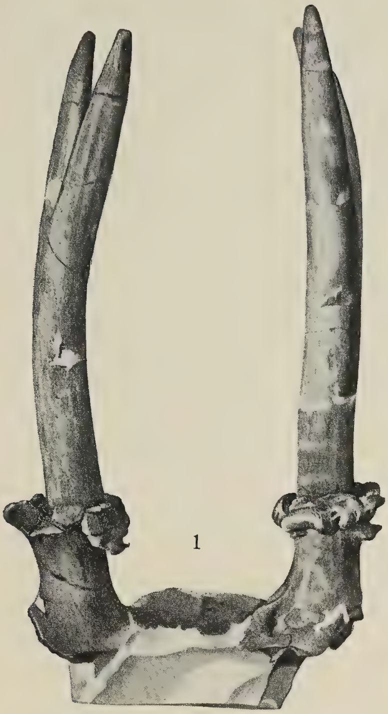
Merycodus hookwayi n. sp.

FIGS. 1, 1a—Front and lateral views of horn-cores; No. 1240; x ½.

FIGS. 2, 2a—Lateral and inferior views of maxillary fragment; No. 710; x 1.

FIGS. 3, 3a and 3b—Lateral and occlusal views of ramus; No. 1257; x 1.

Calif. Inst. Tech. Coll. Upper Miocene, Tonopah, Nevada.



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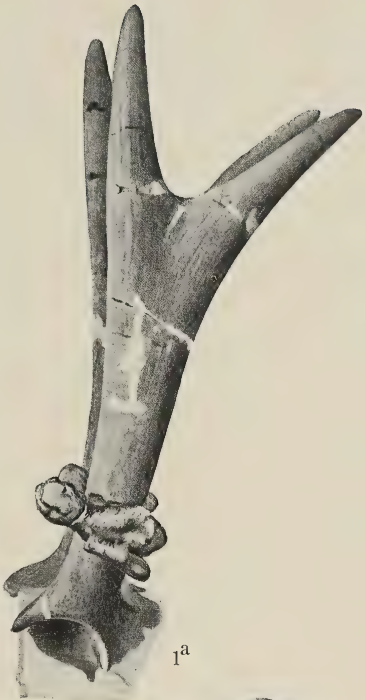

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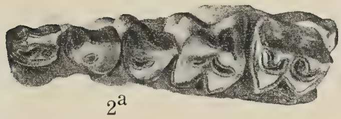

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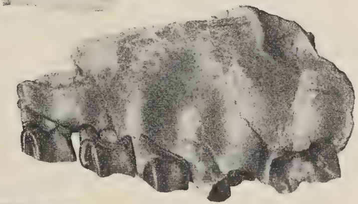

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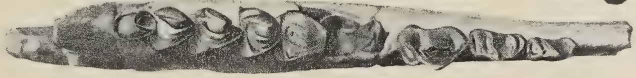

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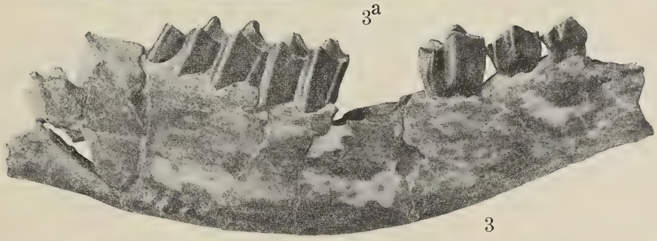

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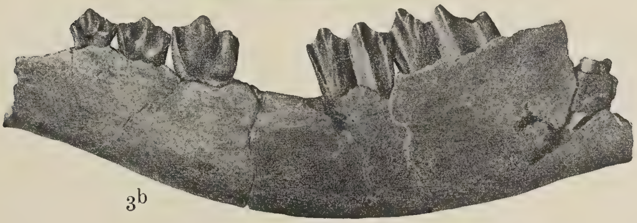

3b

Merycodus hookwayi n. sp.

CONTRIBUTIONS TO PALÆONTOLOGY

II

TWO RODENTS AND A LAGOMORPH FROM THE SESPE OF THE LAS POSAS HILLS, CALIFORNIA

By Robert W. Wilson

[Issued July 1934]

CONTENTS

Page
Introduction 13
Description of Material 13
  Sespemys thurstoni n. gen. and n. sp 13
    Generic and Specific Characters 13
    Description 13
    Comparisons 14
  Sciurid? species 16
  Palæolagus? species 16

TWO RODENTS AND A LAGOMORPH FROM THE SESPE OF THE LAS POSAS HILLS, CALIFORNIA

INTRODUCTION

One of the largest vertebrate assemblages to be recorded from the Sespe deposits of Southern California, representing an upper Oligocene age, was obtained by the California Institute of Technology in the Las Posas Hills of southern Ventura County. The description of this fauna by Dr. Chester Stock is now in progress.[1] The author of the present paper has been granted the privilege of describing the rodents and lagomorphs from this locality. I wish to thank Dr. Stock, not only for permission to study the material, but for a critical reading of the manuscript. The photographs reproduced in the plate have been carefully retouched by Mr. John L. Ridgway.

DESCRIPTION OF MATERIAL

Sespemys thurstoni n. gen. and n. sp.

Holotype—No. 1397, Calif. Inst. Tech. Coll. Vert. Pale., a fragmentary left ramus with $P\overline{4}$, $M\overline{2}$, and $M\overline{3}$.

Paratype—No. 464, Calif. Inst. Tech. Coll. Vert. Pale., a right ramus with $P\overline{4}$–$M\overline{2}$.

Locality—Kew Quarry, Locality 126, C. I. T. Vert. Pale.

Generic and Specific Characters

Mandibular incisor broad, anterior face flat. Anterior border of masseteric fossa prominent and ridged, terminating beneath the posterior border of $M\overline{1}$. Anterior marginal ridge of lower molars forming the principal element in the anterior crest. Protolophid a minor element in the anterior crest and consisting of a short spur only. Basins of molar teeth shallow and extensive but broken by hypolophid. Hypolophid present as a distinct loph connecting externally with protoconid-hypoconid ridge. Metastylid present in cheek-teeth. Metaconid of $P\overline{4}$, in respect to corresponding cusp in *Ischyromys*, more anterior in position. The species is named in honor of the late James E. Thurston, in appreciation of his important services during the progress of the Sespe excavations.

Description

The ramus in *Sespemys thurstoni* is heavy, especially the anterior portion. The masseteric fossa terminates beneath the posterior border of $M\overline{1}$. The anterior border of the fossa tends to be distinct and ridged. In No. 464

---

[1] C. Stock, Proc. Nat. Acad. Sci., vol. 18, 550–554, 2 figs., 1932; Carnegie Inst. Wash. Pub. No. 440, art. 3, 15–28, 4 pls., 1933; *ibid*, art. 4, 29–41, 3 pls., 1933.

this character is quite distinct and the fossa is much more pronounced than in *Ischyromys.* The mandibular incisor is broad, and the anterior face is flat, suggesting the Castoridæ and the Geomyidæ, rather than the Sciuridæ.

The fourth lower premolar is subtriangular in outline. The trigonid possesses a rather large metaconid with a smaller protoconid, the two cusps becoming subequal with wear. A short spur extends inward from the protoconid. A fairly strong anteroposterior ridge connects the protoconid and hypoconid. The entoconid is distinct from the hypoconulid ridge, and a loph connects the former with the protoconid-hypoconid ridge. The hypoconulid ridge is strong and runs internally from the hypoconid along the posterior margin of the tooth. In No. 1397, the apparent presence of the hypoconulid is indicated by a swelling in the enamel. The hypoconulid ridge is separated from the entoconid by a sharp valley. A small metastylid is present between the metaconid and entoconid. This cusp shows a variable development in all of the cheek-teeth.

Little difference is to be noted between the first and second molars. The teeth are subquadrate in outline with broad shallow basins, partly interrupted by transverse lophs. A strong, anterior marginal ridge is present, but the protolophid is represented by a small spur only. The metaconid is anterior to the protoconid. A distinct metastylid is present. The entoconid connects with the protoconid-hypoconid ridge by means of a strong hypolophid, but is separated from the well-developed hypoconulid ridge of the hypoconid by a distinct valley.

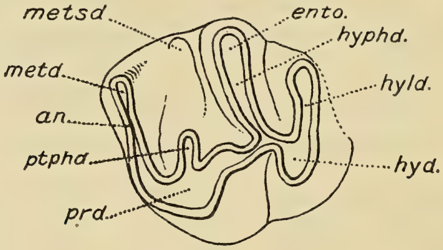

FIG. 1—*Sespemys thurstoni* n. gen. and n. sp. Left M$\overline{2}$, approx. x 9. *Ento.*, entostylid; *hyphd.*, hypolophid; *hyld.*, hypoconulid; *hyd.*, hypoconid; *prd.*, protoconid; *ptphd.*, protolophid; *an.*, anterior marginal ridge; *metd.*, metaconid; *metsd.*, metastylid. These terms do not imply a homology of cusps, but are used simply for convenience.

M$\overline{3}$ is essentially similar to the first two molars. However, the talonid is narrower, the metastylid slightly more distinct, and the metaconid is somewhat more anterior in position.

COMPARISONS

That Nos. 1397 and 464 represent the same species may be subject to some doubt. The masseteric fossa of the former is not so sharply defined, nor is the jaw so deep, at least so far as can be determined in the fragmentary specimen. No differences exist in the molar teeth, but in the fourth lower premolar some differences may prevail, chiefly in the relative size of protoconid with reference to the metaconid. However, it must be stated that the genotype represents a somewhat younger individual than No. 464, and age may therefore account for the apparent differences. Whatever relationships may be indicated by additional material, a comparison of the two existing specimens hardly yields differences which may be used with certainty, and for the present both are regarded as representing the same species.

The new genus is apparently best assigned to the Ischyromyidæ, as this family is defined by Matthew.[1] The position of the anterior border of the masseteric fossa agrees with that in observed specimens of *Ischyromys.* A distinct entoconid and the imperfect development of crests on a sciurid pattern are additional features which place *Sespemys* in this family. However, in development of the anterior marginal ridge on the lower molars and in the basined character of the cheek-teeth, *Sespemys* seems closer to certain members of the Sciuridæ of Troxell[2] than to *Ischyromys* itself.

The new genus *Sespemys,* when compared with *Ischyromys,* presents the following differences: Masseteric fossa more pronounced, although this character is not well shown in the genotype. Lower incisor much broader. In P$\bar{4}$, entoconid connected to protoconid-hypoconid ridge by a distinct loph; metastylid present; metaconid more anterior in position. In the molars, the principal anterior cross-crest is formed chiefly by the anterior marginal ridge, and not by the protolophid; teeth more basined and basins shallower; metastylid present; cheek-teeth less hypsodont; cross-crests in general not so strongly developed.

Measurements (*in millimeters*)

	Sespemys thurstoni Genotype No. 1397 C. I. T. Las Posas Sespe	*Sespemys thurstoni* Paratype No. 464 C. I. T. Las Posas Sespe
Length of diastema		6.8 (a)
Depth of ramus below P$\bar{4}$		8.8
I, transverse diameter		2.6
P$\bar{4}$, anteroposterior diameter	3.1	3.0
P$\bar{4}$, transverse diameter	2.8	2.8
M$\bar{1}$, anteroposterior diameter		2.5
M$\bar{1}$, transverse diameter		2.9
M$\bar{2}$, anteroposterior diameter	2.6	2.6
M$\bar{2}$, transverse diameter	2.9	3.0
M$\bar{3}$, anteroposterior diameter	2.7	
M$\bar{3}$, transverse diameter	2.7	
P$\bar{4}$–M$\bar{2}$, alveolar length		8.9
P$\bar{4}$–M$\bar{3}$, alveolar length	12.1 (a)	

(a) approximate.

Adequate illustrations or descriptions of the genus *Prosciurus* are unfortunately not available. However, the Sespe form would seem to be generically distinct from *Prosciurus.* The dentition in the latter, as stated by both Matthew and Cope, is rather close to that of *Sciurus.*[3] No mention is made of the presence of a well-developed hypolophid. Cope records the presence of a cusp in the lower molars of *Prosciurus relictus.*[4] This structure may correspond to the distinct entoconid in *Sespemys* or to a metastylid, although it is rather prominent to be the latter. Since Cope states that he first referred the type of *P. relictus* to *Paramys,* a form with distinct entoconids in the lower molars, the former designation may be correct. On the other hand, mesostyles are present in the upper molars of *Prosciurus vetustus* Matthew, and the cusp in question may be somewhat anterior in position for an entoconid. No trace of a hypolophid can be seen in Cope's figure of *P. relictus.*[1]

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[1] W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 28, art. 6, 44–45, 1910.

[2] E. L. Troxell, Amer. Jour. Sci., 5th ser., vol. 5, art. 32, 395, fig. 23, 1923.

[3] W. D. Matthew, *ibid,* 63, 1910; E. D. Cope, Report U. S. Geol. Surv. Terr., vol. 3, *Tertiary Vertebrata,* book 1, 816–819, 1884.

[4] E. D. Cope, *ibid,* 818, 1884.

On the whole, *Sespemys* seems structurally to occupy a position somewhat intermediate between *Ischyromys* and *Sciurus*, but since *Prosciurus*, a more direct ancestor to *Sciurus*, occurs at approximately the same geologic horizon, *Sespemys* can not be regarded as an ancestor of *Sciurus*. Moreover, both *Sespemys* and *Ischyromys* are too far removed from the main line of sciurid evolution to have given rise to forms close to the Recent tree-squirrel. The Las Posas Hills genus possibly represents an aberrant ischyromyid, situated nearer the main line of evolution of the squirrels than *Ischyromys*. A more complete statement must await not only additional material of *Sespemys*, but also a better understanding of the relationships of the early sciuromorphs.

Sciurid? species

A fragment of right ramus with incomplete $P\overline{4}$, No. 1513 C. I. T. Coll. Vert. Pale., represents a sciurid or prosciurid type distinct from *Sespemys thurstoni*. In so far as it can be determined in the fragment available, the masseteric fossa hardly extended forward to a point beneath $M\overline{1}$, but must have terminated posterior to this tooth. This character indicates an ischyromyid, but the incomplete $P\overline{4}$ shows typical sciurid characters. In view of the fragmentary character of the specimen, definite allocation of No. 1513 to the Sciuridæ or to the Ischyromyidæ of Matthew remains somewhat arbitrary. The fourth lower premolar resembles *Sciurus* in general lowness of the cusps. However, in depth of basin and in the identation of the external margin of the tooth, the specimen is perhaps more like other members of the Sciuridæ.

Measurements (*in millimeters*)

$P\overline{4}$, anteroposterior diameter	1.9
$P\overline{4}$, transverse diameter	1.7

Palæolagus? species

This early lagomorph is represented in the collections from the Las Posas Hills by a single specimen, No. 1512 C. I. T. Coll. Vert. Pale., an incomplete left ramus with $P\overline{3}$ to $M\overline{2}$. Unfortunately, the specimen is so poorly preserved that characters important for its identification are almost wholly lacking.

In No. 1512, the incisor apparently originates below $M\overline{1}$, as in *Palæolagus*. The anterior edge of the masseteric muscle scar is situated beneath $M\overline{2}$. $P\overline{3}$ is in an extremely unsatisfactory state of preservation, but shows one strong external enamel inflection and lacks the small secondary external inflection characteristic of *Archæolagus*. The presence or absence of this inflection may remain uncertain, in view of the preservation of the tooth, but the external wall possesses two ridges instead of three as found in *Archæolagus*. The occlusal surface of the tooth exhibits a structure which may be regarded as an internal enamel inflection, but this is not at all certain. The internal wall of the tooth forms a shallow groove, extending partly down the side, and this may further suggest the presence of an inflection. However, the presence or absence of the internal enamel inflection can not be definitely established. *Palæolagus haydeni* ordinarily exhibits a single external and internal inflection of the enamel in the third lower premolar. With sufficient wear the internal inflection disappears. The external inflection eventually disappears also, except for a groove down the side of the tooth.

---

[1] E. D. Cope, *ibid*, pl. 65, fig. 35b, 1884.

The enamel inflections in $P\overline{3}$ of the Las Posas lagomorph occur at about the mid-point of the tooth, dividing it into two semicircular lobes, the posterior one more elliptical, the anterior one apparently slightly drawn out at its anterior tip. The cheek-teeth $P\overline{4}$–$M\overline{2}$ show the posterior lobes joined to the anterior lobes at the buccal borders.

Measurements (in millimeters)

Length of diastema	10.4
Depth of ramus beneath $P\overline{3}$	7.2 (a)
$P\overline{3}$–$M\overline{2}$, alveolar length	8.5
$P\overline{3}$, anteroposterior diameter	1.8
$P\overline{3}$, transverse diameter	1.2
$P\overline{4}$, anteroposterior diameter	1.9
$P\overline{4}$, transverse diameter	2.0
$M\overline{1}$, anteroposterior diameter	2.2
$M\overline{1}$, transverse diameter	2.3
$M\overline{2}$, anteroposterior diameter	2.3
$M\overline{2}$, transverse diameter	2.3

(a) approximate.

PLATE 1

Sespemys thurstoni n. gen. and n. sp.

FIG. 1—Fragmentary left ramus with P$\overline{4}$, M$\overline{2}$, and M$\overline{3}$, type specimen, No. 1397 Calif. Inst. Tech. Coll. Vert. Pale. Approx. x 4.

FIGS. 2, 2a, and 2b—Right ramus with P$\overline{4}$–M$\overline{2}$, paratype specimen, No. 464 Calif. Inst. Tech. Coll. Vert. Pale. Fig. 2, lateral view, approx. x 1.3; figs. 2a, 2b, occlusal views, approx. x 1.3 and x 5.

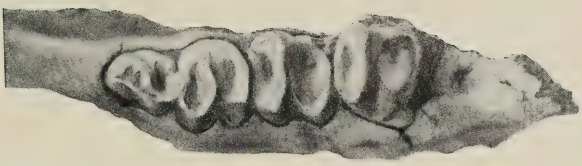
Sciurid? sp.

FIG. 3.—Fragment of right ramus with P$\overline{4}$, No. 1513 Calif. Inst. Tech. Coll. Vert. Pale. Approx. x 4.

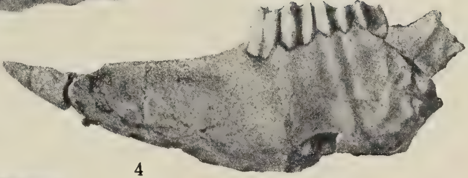
Palæolagus? sp.

FIGS. 4 AND 4a—Fragmentary left ramus with P$\overline{3}$–M$\overline{2}$, No. 1512 Calif. Inst. Tech. Coll. Vert. Pale. Fig. 4, lateral view, approx. x 2; fig. 4a, occlusal view, approx. x 5.

Sespe Oligocene, Las Posas Hills, California.



4a



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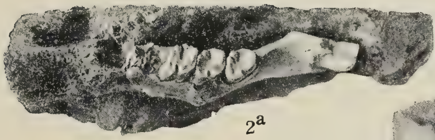

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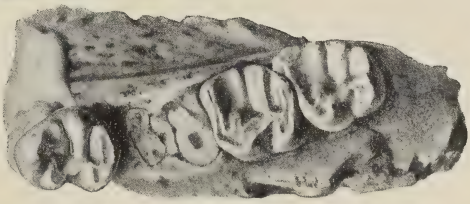

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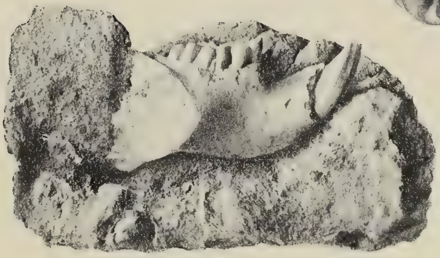

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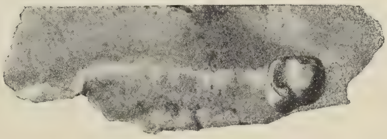

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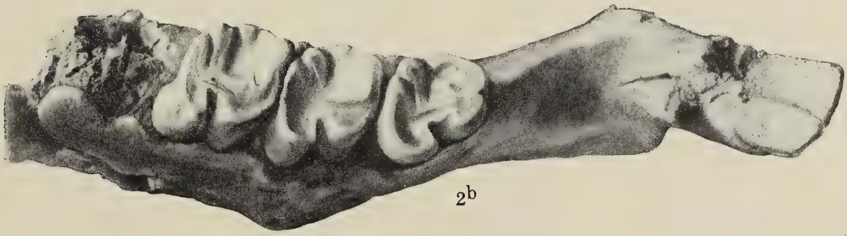

2b

CONTRIBUTIONS TO PALÆONTOLOGY

III

A NEW SPECIES OF DIPOIDES FROM THE PLIOCENE OF EASTERN OREGON

By Robert W. Wilson

With one plate and one text-figure

[Issued December 20, 1934]

CONTENTS

Page

Introduction.......... 21

Dipoides stirtoni n. sp.......... 21

Description of Material.......... 21

Comparisons with Known Species.......... 26

Comparisons with Closely Related American Forms.......... 28

A NEW SPECIES OF DIPOIDES FROM THE PLIOCENE OF EASTERN OREGON

INTRODUCTION

Numerous remains of castoroid rodents from the Tertiary of North America have been referred to the Old World genus *Dipoides* Jaeger. Apparently, most of the material represents types generically distinct from *Dipoides,* and the genus is actually represented by very few specimens of fragmentary character. It is not the purpose of this paper, however, to present the distinguishing characters which separate the true *Dipoides* from other American beavers with simplified dental pattern, but to describe remains of a *Dipoides* species collected by California Institute of Technology field parties in Pliocene beds in the region of Rome, Oregon. R. A. Stirton, of the University of California, has made a study of the taxonomy and relationships of members of the beaver group and his report on the Castoridæ is now in press.

Dipoides stirtoni n. sp.

Geological horizon and locality—Pliocene lake beds exposed along the Crooked Creek drainage, tributary to the Owyhee River, 5 miles southwest of Rome, Malheur County, Oregon.

Type specimen—A left ramus with $P\overline{4}$-$M\overline{3}$, No. 1662, Calif Inst. Tech. Coll. Vert. Pale., Plate 1, figs. 10, 10a.

Referred material—Several fragmentary lower jaws, including two rami of immature individuals with the deciduous molar preserved; a fragment of maxillary with $M\underline{1}$; numerous isolated upper and lower cheek-teeth and incisors; and a number of fragmentary skeletal elements.

Specific characters—Cheek-teeth prismatic. $P\overline{4}$ with antero-internal fold well developed and extending to base of tooth. $P\underline{4}$ with at least two external grooves extending to the base of the tooth, representing two enamel infolds as seen in occlusal view. $M\overline{1}$ and $M\overline{2}$ sub-equal. Molars relatively narrower than in *Dipoides majori* Schlosser. Size about as in *Dipoides* cf. *majori* from Ertemte and Olan Chorea, Mongolia. The species is named in honor of Mr. R. A. Stirton for his work on fossil beavers.

DESCRIPTION OF MATERIAL

While numerous isolated cheek-teeth, representing the upper dentition, are available from the Rome area, the assignment of these teeth to a definite position in the maxillary is in most cases not possible. Even the fourth upper premolar, generally determined without much difficulty, does not seem to be clearly separable from the first molar. Moreover, in spite of the prismatic structure of the cheek-teeth accompanied by extreme hypsodonty, the dental pattern apparently undergoes considerable modification with wear, or there is considerable individual variation, which is not likely, or both. Hence, the following description of the upper dentition is necessarily subject to some doubt.

The fourth upper premolar is presumably the largest tooth in the superior grinding series. It is rather sharply curved backward and outward. Normally this tooth (Plate 1, fig. 5) possesses two external and one internal inflections of the enamel with corresponding grooves on the side, which extend to the base of the tooth. The antero-external and the internal inflections are adjacent and separated by a narrow isthmus of dentine. In rare cases, this isthmus is cut through and the antero-external and internal inflections are confluent (Plate 1, fig. 4). In young specimens (Plate 1, fig. 3) a third external inflection of the enamel, which is posterior to the other two, is present and appears as a fold in the posterior outwardly directed enamel loop. This fold is sometimes present with an accompanying groove on the side of the tooth which may or may not extend to the base, or without the groove, or as an isolated enamel islet. Apparently in P$\underline{4}$ of *D. stirtoni* at least two external folds of the enamel are always present and reduction to one external fold and one internal fold does not take place.

The first upper molar is smaller than the preceding tooth and probably less curved outward. In No. 1668 (Plate 1, fig. 2), a portion of the maxillary with apparently this tooth, a single external and an internal inflection of the enamel are present. This stage, however, seems to be present only after more or less wear. In another tooth, No. 1691 (Plate 1, fig. 6), identified as M$\underline{1}$ or M$\underline{2}$ and more probably the former, isolated lakes are shown, representing the first and third external inflections. Hence, at some stage of wear M$\underline{1}$ must have a pattern considerably like that of P$\underline{4}$.

The second upper molar has not been positively identified. A tooth, No. 1692 (Plate 1, fig. 9), tentatively determined as M$\underline{2}$, shows a single external and internal inflection. In the young individual the occlusal pattern of the tooth may have had other inflections such as are shown in the first molar.

Several isolated grinding teeth have been tentatively identified as third upper molars. These teeth, Nos. 1687 to 1690, possess patterns unlike any others in the grinding series and agree to some extent with those in a *Dipoides* skull described by Young[1] from northern China. These teeth are curved backward but not noticeably outward. No. 1688 possesses an isolated lake corresponding to the first external inflection and two external folds corresponding to the second and third external inflections. These latter are confluent internally. The usual internal inflection is also present. This condition indicates the presence at an earlier stage of wear of three external and one internal inflections of the enamel. In No. 1687 (Plate 1, fig. 1), which shows a later stage of wear than No. 1688, the enamel lake has disappeared and the most posterior external inflection has become isolated from the outside giving a pattern somewhat like an inverted ∩. In still later stages of wear the tooth apparently assumes a pronounced sigmoidal pattern.

The superior incisors differ noticeably from those of *Castor* in more rounded anterior face. In the Recent beaver the incisors are flattened.

The lower jaw is relatively a little shorter and stouter than in *Castor* and possesses the following differences: (1) Angle with distinct descending portion; (2) area for muscle attachment at the symphysis extends posteriorly past chin and terminates about opposite the anterior portion of M$\overline{1}$; (3) depression between alveolar border and coronoid greater than in *Castor;* and (4) termination of the incisor apparently somewhat higher in the jaw. Additional differences may exist, but the fragmentary character of the fossil remains make these characters difficult to determine.

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[1] Chung-Chien Young, Palæontologia Sinica, Series C, vol. 5, Fasc. 3, 11-13, Taf. 1, figs. 5, 5a, 1927.

The inferior incisors of *Dipoides,* like the superior, have rounded faces as opposed to the flattened incisors of *Castor.*

The fourth lower premolar (Plate 1, fig. 10a) is a large, rather straight tooth characterized by one large external inflection of the enamel and two internal inflections, the posterior one being the deeper. This pattern is very persistent for in only one of twenty-six specimens examined was there any indication of a change with wear. In this single specimen the occlusal surface of the tooth is normal, but the groove on the internal wall of the tooth, corresponding to the antero-internal inflection, extends down to a point about nine-tenths of the way from the wearing surface and stops. The base of the tooth shows a pattern in which the antero-internal inflection appears as an isolated lake.

The first lower molar (Plate 1, fig. 10a) is somewhat smaller than the premolar. The second molar (Plate 1, fig. 10a) is sub-equal in size to the first. Both teeth apparently invariably possess a single external and internal inflection of the enamel.

The last lower molar is somewhat narrower than the first two, but possesses about the same antero-posterior dimensions. It also invariably has one external and one internal inflection of the enamel. In addition, in some specimens, the anterior loop of enamel possesses a small re-entrant fold (Plate 1, fig. 10a). This fold apparently disappears with wear.

The cheek-teeth as a whole are characterized by extreme hypsodonty. At first it was believed that growth was from persistent pulps. However, in eighty-nine cheek-teeth examined, two (incidentally from the same individual) were found in which the bases of the teeth were closing. Very few cases were encountered in which the lateral grooves, representing the enamel folds in the occlusal pattern, did not extend to the base of the teeth. Since changes in tooth pattern by reduction of minor folds apparently took place, the termination of the minor lateral grooves short of the base of the tooth is probably more frequent than observed.

Two fragmentary right lower jaws, Nos. 1663 and 1664, carry the deciduous molar. These teeth are relatively short-crowned with distinct roots, and the lateral grooves are not so persistent as in the permanent teeth, thus tending toward an isolation of the inflections as lakes. Specimen No. 1663 (Plate 1, fig. 11) carries only $DM\overline{4}$. This tooth is a reduced replica of the permanent premolar except that opposite the tip of the external inflection are three isolated lakes arranged in a line. Specimen No. 1664 has $M\overline{1}$ present in addition to $DM\overline{4}$. The deciduous molar represents a stage of wear advanced over No. 1663, since the permanent premolar is present beneath the milk molar, which was not the case in the latter specimen. The enamel lakes opposite the tip of the external inflection are not present, but the antero-internal inflection is represented by an enamel lake.

Several teeth in the collections show patterns in early stages of wear (Plate 1, figs. 7, 7a, 8, 8a). The occlusal patterns seem to be characterized by three inflections from one side and one from the other, and are thus suggestive of the earlier and more primitive casteroids from which *Dipoides* is apparently to be derived. The minor folds which are later lost are represented on the walls of the teeth by lateral grooves which rarely extend very far down the sides.

Numerous fragmentary remains of the skeleton of *Dipoides* are present in the collection (fig. 1). Unfortunately most of the limb elements are incomplete, so that important information relating to the ratios of the lengths of the various limb bones can not be obtained. However, the conclusion was reached that *Dipoides* is certainly not fossorial and, although most of the skeletal elements differ from those of *Castor* in varying degrees of detail, that the genus may be amphibious.

The vertebræ are very poorly preserved. None is flattened as are the tail vertebræ of *Castor*.

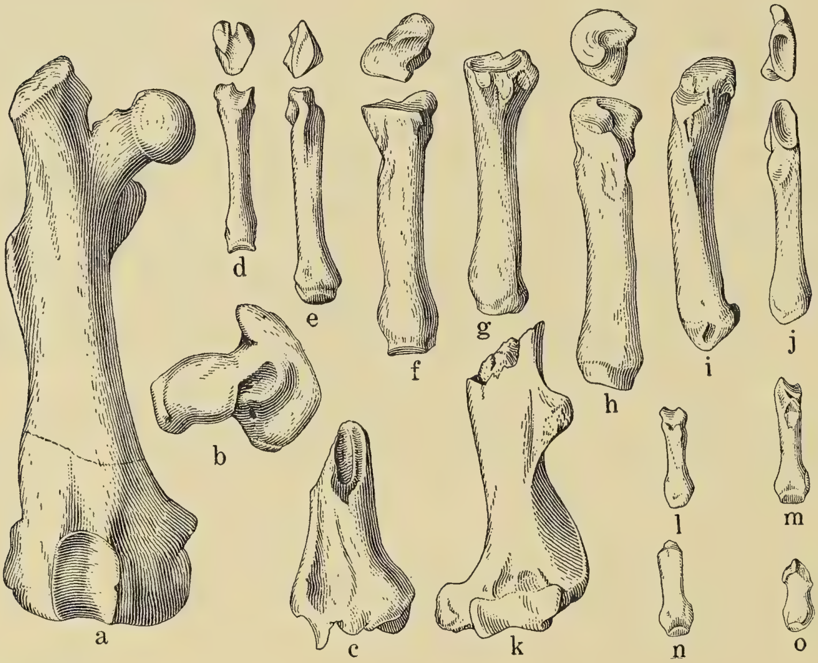

FIG. 1.—*Dipoides stirtoni* n. sp. Limb and foot elements, Nos. 1698 to 1705, 1707, 1715 to 1718 Calif. Inst. Tech. Vert. Pale. Coll., natural size. *a,* femur; *b,* proximal end of tibia; *c,* distal end of fused tibia and fibula; *d,* right metatarsal I; *e,* right metatarsal II; *f* and *g,* right metatarsal III; *h* and *i,* right metatarsal IV; *j,* left metatarsal V; *k,* distal fragment of humerus; *l,* right metacarpal II; *m,* left metacarpal III; *n,* right metacarpal IV; *o,* left metacarpal V.
Rome Pliocene, Malheur County, Oregon.

The humerus is essentially as in *Castor,* although smaller, as are all of the skeletal elements. The element agrees with that of *Castor* in lacking the entepicondylar foramen. The supinator ridge is not so well developed as in such fossorial forms as *Epigaulus.*

The ulna resembles very closely that of *Castor.* The proximal portion of the olecranon process, however, projects internally and the process is elongate transversely rather than in an anteroposterior direction. The element is much less massive than the ulna of *Epigaulus.* The proximal end of the radius is similar to that in *Castor.* The distal portion of the shaft is not so flattened as in the living genus, and the distal articular surface is noticeably concave.

The scapula is incompletely represented. A few fragments of the anterior border are all that have been found. In most of the specimens the corocoid process seems more prominent than in *Castor,* but otherwise no differences were noted.

The manus of *Dipoides,* exclusive of the phalanges, is represented only by a poorly preserved scapho-lunar and the second, third, fourth and fifth metacarpals. Compared to the metacarpals of *Castor* those of the Pliocene genus apparently have less flattened, narrower heads and are somewhat larger, relative to the metatarsals. In *Dipoides* metacarpals II and IV are of nearly equal size. The second metacarpal is longer but the fourth is perhaps more robust. In the Recent beaver, metacarpal IV is both considerably longer and more robust than the second metapodial.

The remains of the pelvis are too fragmentary to be of any value. No differences were observed between the fossil genus and *Castor.*

The shaft of the femur of *Dipoides* is less flattened than in *Castor,* the third trochanter is placed higher on the shaft, the great trochanter overtops the head to a greater extent; and the neck is longer. The patellar surface is also deeper and narrower than in *Castor.*

The femoral articulations of the tibia are somewhat more convex antero-posteriorly than in the comparable element of Castor. In *Dipoides* the proximal tip of the cnemial crest is prominent and projects slightly outward. Hence, there is a wide notch between the external facet and the proximal tip of the cnemial crest. The outline of the articular surface of the distal end is more rectangular than in *Castor* and the posterior process of the tibial-tarsal articular surface is more internal in position. A prominent difference which distinguishes *Dipoides* from *Castor* lies in the distal fusion of the tibia and fibula in the former genus.

The pes of *Dipoides* is represented by a tarsus, complete except for the external and middle cuneiform; all five metatarsals; and most of the phalanges. In the calcaneum, the tuber calcis is relatively shorter than in *Castor,* the facet for articulation with the cuboid is at a more acute angle with the long axis of the bone, and the sustentacular facet is relatively short and parallel to the long axis of the calcaneum. The head of the astragalus is not so flattened transversely as in *Castor* and the neck is shorter. The trochlear surface in the Recent beaver is flatter than in *Dipoides.* The navicular is relatively broader than in *Castor,* and the astragalar surface is elongate transversely instead of more or less antero-posteriorly. The cuboid also is relatively broader than in *Castor.* The facet for articulation of Metatarsal IV is not as concave or as elongate, and the inner facets are more pronounced. The inner cuneiform of *Dipoides* is close to that of *Castor,* but the bone in the former does not narrow so rapidly toward the proximal side and is thus more rectangular.

The metatarsals of *Dipoides* seem to indicate a foot which was not so spreading as that of *Castor.* Moreover, these elements are not so well developed relative to the metacarpals as in the latter genus, indicating perhaps a less amphibious habit, if indeed it is to be assumed that *Dipoides* was semiaquatic. The metatarsals of *Dipoides* are not noticeably flattened distally, as seems to be the case in the pes of *Castor* examined. There are besides many differences of detail in which the metatarsals of the two genera differ. The phalanges of *Dipoides* are also not so flattened as in the Recent beaver.

COMPARISONS WITH KNOWN SPECIES

At the present time only four species of this genus are known; *Dipoides problematicus, D. sigmodus, D. majori* and the present species. Species from the North American Tertiary such as *tortus, lecontei* and *curtus* apparently do not represent *Dipoides. D. problematicus,* the type species, and *D. sigmodus* are from the Tertiary of Europe, *D. majori* from Mongolia and China.

The type species, *Dipoides problematicus* from the Bohnerzen of Salmendingen,[1] is a smaller form than the Rome species. Illustrations of *D. problematicus* show teeth which are less prismatic than those of *D. stirtoni,* that is to say the teeth are narrower at the top than at the base. Moreover, in spite of the fact that the teeth figured by Schlosser are open at the base of the crown, he describes them in the text as possessing roots.[2] If many specimens of *D. problematicus* are rooted, this character seems to distinguish the type species from the New World form. As mentioned before, closure of the pulp cavities is rare in the Rome material, and even in the single individual in which this character is shown, no roots have formed. It is not very probable that all of the teeth studied are from young individuals.

Dipoides sigmodus is from the fluviatile marls under the Palace of Justice of Montpellier.[3] This species has a longer tooth row than *D. stirtoni* and P$\overline{4}$ and M$\overline{1}$ are sub-equal in size.[4] In P$\overline{4}$ of a ramus of *D. sigmodus* the antero-internal fold is represented as an isolated lake. However, in another specimen P$\overline{4}$ is normal.[5] This may indicate a greater tendency for the fourth lower premolar to be S-shaped than in *D. stirtoni.* In the Rome species, as mentioned previously, only a single specimen shows an isolated lake in place of a re-entrant fold, and this isolation occurs below the level of the present wearing surface of the tooth.

The type of *Dipoides majori* Schlosser is a unique lower jaw with M$\overline{1}$–M$\overline{3}$ and alveolus for P$\overline{4}$.[6] In view of the incompleteness of the type, comparisons with our species are difficult to make. In size it agrees with large representatives of *D. stirtoni.* The molar series increases in size from front to back, whereas in the Rome type M$\overline{1}$ and M$\overline{2}$ are sub-equal. The molars of *D. stirtoni* are on the average narrower than in the Chinese type. This is most noticeable in M$\overline{1}$, least noticeable in M$\overline{2}$. Schlosser subsequently described as *Dipoides* cf. *majori*[1] some isolated teeth and limb bones from Ertemte and Olan Chorea, Mongolia. This material apparently represents a type somewhat smaller than *D. majori* and nearly comparable in size to the average *D. stirtoni.* Schlosser believed that the Chinese form might represent an individual surpassing the average in size, and refrained from erecting a new species. Schlosser's description of the upper cheek-teeth agrees with that based on characters displayed by *D. stirtoni,* when variation due to wear is taken into consideration. His figures[2] do not appear to check his description but this may be due to an error in the figures.

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[1] Max Schlosser, Geol. Pal. Abh., Neue Folge, Band 5, Helt 3, 21-23, Taf. 1, 1902.

[2] *Ibid.,* 21, 1902.

[3] Paul Gervais, Zool. et Pal. Françaises, Paris, 21-22, pl. 1 fig. 13, pl. 8, fig. 10b, 1859.

[4] I am indebted to R. A. Stirton of the University of California for important information concerning *D. sigmodus.* Mr. Stirton kindly permitted me to use his unpublished manuscript concerning the genus *Dipoides.*

[5] Paul Gervais, *loc. cit.,* pl. 1 fig. 13, pl. 8 fig. 10b, 1859.

[6] Max Schlosser, Abh. bayr. Ak., der Wiss., II, Cl. 22, Bd. 1, Abth., 40-42, Taf. II, figs. 14, 14a, 1903.

Schlosser points out as a difference between *D. problematicus* and *D. majori* that the superior molars of the former "differ from those found at Ertemte and Olan Chorea by the separation of the median out fold from the inner fold by a thin bridge of dentine."[3] The only dentinal bridge that can be seen in the figures of *D. problematicus* is that formed by the first internal and external re-entrant angles. If this is the bridge referred to, the superior molars of *D. stirtoni,* possessing two external and one internal inflections of the enamel, agree to this extent with those of the European form and differ with those of the Asiatic type. Two specimens present in the Rome collections, however, show this bridge cut through. The fourth lower premolar of *Dipoides* cf. *majori* may differ from that of *D. stirtoni* in lacking the anterior internal inflection. A figure of P$\overline{4}$ shows no inflection but a second figure does.[4] His text does not indicate very clearly which pattern is the most characteristic. Schlosser[5] figures a number of skeletal elements of *Dipoides* cf. *majori.* This material agrees with that from North America in size and in other characters as well. There are apparently minor differences to be noted, but actual comparison of material might serve to eliminate even these.

Young has described a skull of *Dipoides* from north China as *D. majori.*[6] In this specimen the superior cheek-teeth possess only a single external and internal inflection. Of the described species of *Dipoides,* the Asiatic species *D. majori* and its referred material is perhaps closest to *D. stirtoni.* However, the proportions of the lower molars appear to be slightly different, and in addition *D. majori* is probably to be distinguished, as suggested in the above comparisons, by a tendency to develop a simpler pattern in the cheek-teeth. The development of a less complex pattern would indicate a more advanced species. In any event, the geographic separation serves to lessen the possibility of specific identity.

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[1] Max Schlosser, Palæontologia Sinica, Series C, vol. 1, Fasc. 1, 27-30, pl. II, figs. 11, 29-41, 1924.

[2] Max Schlosser, *ibid.,* pl. II, figs. 29a, 31, 1924.

[3] *Ibid.,* 28, 1924.

[4] *Ibid.,* pl. II, figs. 30, 32, 1924.

[5] *Ibid.,* pl. II, figs. 11, 34-41, 1924.

[6] Chung-Chien Young, *loc. cit.,* 1927.

COMPARISONS WITH CLOSELY RELATED AMERICAN FORMS

Two additional localities in the Tertiary of western North America have furnished *Dipoides* material which appears to be related to that of *D. stirtoni.* Louise Kellogg has described a P$\overline{4}$ and M$\overline{1}$ of *Dipoides* from Thousand Creek, Nevada, as *Dipoides,* sp. probably new.[1] The Thousand Creek specimens may possibly represent *Dipoides stirtoni,* although with the present incomplete remains it is impossible to determine this. In the Rattlesnake collections of the California Institute of Technology from eastern Oregon are two fragmentary rami, a left lower jaw with P$\overline{4}$, M$\overline{2}$, and M$\overline{3}$, No. 1339 C.I.T. Coll. Vert. Pale., and a right lower jaw with M$\overline{1}$, No. 1340 C.I.T. Coll. Vert. Pale. *Dipoides stirtoni* apparently is to be distinguished from these specimens by the possession of a deeper, more massive ramus, and possibly by more hypsodont dentition. It might be mentioned in this connection that the type of *D. stirtoni* selected, although the most perfectly preserved specimen in the Rome collection, is somewhat below average in size.

TABLE 1—*Table of measurements (in millimeters)*

	C. I. T. No. 1662 Rome, Ore.	C. I. T. No. 1665 Rome, Ore.	C. I. T. No. 1666 Rome, Ore.	C. I. T. No. 1667 Rome, Ore.
Length of lower tooth row	20.3	21.8	22.0	...
P$\overline{4}$, anteroposterior diameter	6.0	6.5	6.5	6.4
P$\overline{4}$, transverse diameter	4.7	4.8	5.2	5.1
M$\overline{1}$, anteroposterior diameter	4.8	5.2	4.8	5.6
M$\overline{1}$, transverse diameter	4.9	4.7	5.1	4.9
M$\overline{2}$, anteroposterior diameter	4.8	5.2	4.7	5.8
M$\overline{2}$, transverse diameter	4.8	4.6	5.0	4.9
M$\overline{3}$, anteroposterior diameter	5.1	4.8	5.3	...
M$\overline{3}$, transverse diameter	4.3	4.2	4.3	...
Length of diastema between I and P$\overline{4}$	*a*18.2	...	*a*17.7	...

a, approximate.

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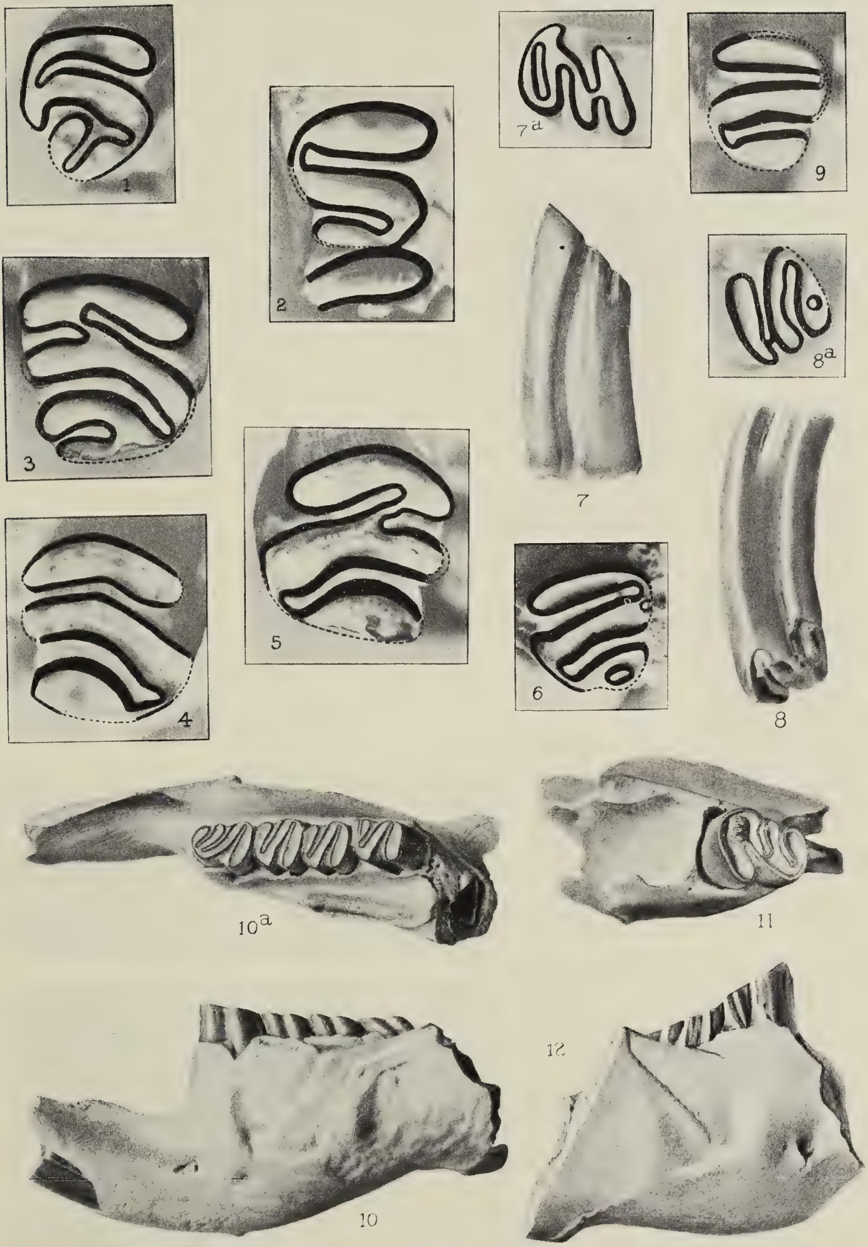
[1] Louise Kellogg, Univ. Calif. Publ., Bull. Dept. Geol., vol. 5, No. 29, 431, fig. 14, 1910.



Dipoides stirtoni n. sp.

Fig. 1, $\mathrm{M}\underline{3}$?, No. 1687; fig. 2, fragmentary right maxillary with $\mathrm{M}\underline{1}$, and incomplete $\mathrm{M}\underline{2}$, No. 1668; fig. 3, $\mathrm{P}\underline{4}$, No. 1695; fig. 4, $\mathrm{P}\underline{4}$, No. 1697; fig. 5, $\mathrm{P}\underline{4}$, No. 1696; fig. 6, $\mathrm{M}\underline{1}$?, No. 1691; figs. 7, 7a, little-worn cheek-tooth, No. 1693; fig. 7, lateral view, fig. 7a, occlusal view; figs. 8, 8a, little-worn cheek-tooth, No. 1694; fig. 8, lateral view; fig. 8a, occlusal view; fig. 9, $\mathrm{M}\underline{2}$?, No. 1692. All figures approximately x 4.

Figs. 10, 10a, left ramus with $\mathrm{P}\overline{4}$-$\mathrm{M}\overline{3}$, type specimen, No. 1662, approximately x 1.33; fig. 11, fragmentary right ramus with $\mathrm{DM}\overline{4}$, No. 1663, approximately x 2.66; fig. 12, fragmentary right ramus with $\mathrm{P}\overline{4}$-$\mathrm{M}\overline{2}$, No. 1667, x 1.33.

Calif. Inst. Tech. Coll. Vert. Pale. Pliocene, Rome, Malheur County, Oregon.

CONTRIBUTIONS TO PALÆONTOLOGY

IV

PLANTS IN THE DUNG OF NOTHROTHERIUM FROM GYPSUM CAVE, NEVADA

By J. D. Laudermilk and Philip A. Munz

With eleven plates

[Issued December 20, 1934]

CONTENTS

Page

Introduction 31

Composition of the Dung Balls 31

Study of Existing Floras 32

Macroscopic Description of Ground Sloth Dung 33

Examination of the Minus Twenty Mesh Fines 34

Identification of the Larger Fragments 35

Differences in Plant Assemblages occurring in Dung of Ground Sloth and Wild Burro . 36

Conclusions 36

PLANTS IN THE DUNG OF NOTHROTHERIUM FROM GYPSUM CAVE, NEVADA

INTRODUCTION

Gypsum Cave is situated some eighteen miles east of Las Vegas, Nevada, at an elevation of 1500 feet and is surrounded by a typically sparse desert flora. During the years 1930 and 1931 the cave was systematically excavated by joint expeditions from the Southwest Museum, Los Angeles, California, and the California Institute of Technology. Among the organic remains uncovered were parts of skeletons, desiccated hide, hair and other integumental structures of the extinct ground-sloth, *Nothrotherium*. In addition were found skeletal remains of camels and of other vertebrates.

During the progress of the excavations several layers of dung were noted, overlying and intermixed with the sloth remains. A large part of this material, which in most cases is in a remarkable state of preservation, was identified as that of *Nothrotherium*. The present report is based upon specimens obtained from the palæontological collections of the California Institute of Technology.

Identification of the plant tissues in the sloth dung seemed particularly desirable in order to answer two questions: (1) What was the flora of the region at the time the sloth inhabited the cave, and (2) does the identification of the flora cast any light on the climatic conditions at the time the gound-sloth lived?

Some identifications of the plant remains comprising the sloth dung were presented by Dr. Arthur D. Howard in Mr. Harrington's book [1] on Gypsum Cave, published in 1933 by the Southwest Museum. Dr. Howard's list, as given in the report, consists of the following:

1. Gymnospermæ—Pine Family—bark—(possibly "Mexican tea" *Ephedra viridis* Cov.)
2. Joshua Tree—*Yucca brevifolia* Engelm. Recognized by chitinous saw-tooth leaf edges. Also represented by much fiber, some still attached to epidermis.
3. Rushes or grasses—*Juncus* or *Graminæ*. Epidermis.
4. Saltbush, *Atriplex sp.* One or more species present. Compare Spiny Saltbush *A. confertifolia* Wats. Recognized by fruits and fibrous portion, or bases of fruit bracts.

COMPOSITION OF THE DUNG BALLS

Volumetric determinations were made of two 100 c.c. samples of the dung materials, in order to determine approximately the proportion of yucca tissue to other plant fragments present. The determinations indicated that fully 80 per cent of the material consisted of yucca. The remaining 20 per cent was made up of species listed in table 1, as well as of some unidentified material.

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[1] M. R. Harrington, *Gypsum Cave, Nevada,* Southwest Museum Papers, No. 8, 193-194. 1933.

STUDY OF EXISTING FLORAS

Before attempting any identifications of the plant remains in the ground-sloth material, the writers, in company with Dr. A. O. Woodford of the Geology Department, Pomona College, visited Gypsum Cave and vicinity (Plate 1). Specimens of the flora available at the time (May 20 and 21, 1933) were collected. This material was killed and fixed in the field in order to preserve the histological structures with as little alteration as possible. Formalin-alcohol (Lynds-Jones formula) was used for the purpose. Approximately thirty-five specimens were collected. Part of the plants comprising this collection came from a locality in the Clark Mountains, California, approximately 42 miles southwest of Gypsum Cave and at an elevation of about 5000 feet. The plants collected at this locality represent, in most cases, types which prefer a higher altitude and more abundant rainfall. *Yucca brevifolia* (Joshua tree), *Yucca baccata* (blue yucca), *Agave utahensis* (mescal) and *Ephedra nevadensis* (Mexican tea) were among those obtained. With the exception of *Ephedra,* which flourishes at both localities, none of this group grows in the vicinity of the cave at the present time. This point is important and will be considered later in the paper.

The alcoholic material was brought to the laboratory for study, and both microscopic and macroscopic methods were applied. For the latter work, which fell more especially within Dr. Munz' field, the extensive herbarium of Pomona College was available.

A systematic histological study of the preserved material was made. Permanent type slides, demonstrating the tissue elements of each specimen were prepared. The type slides included both transverse and longitudinal sections of stems, leaves, petioles, etc., as well as sections of the epidermis separated by maceration methods. Type slides were also made of the pollen, hairs and of the calcium oxalate crystals so abundant in the Joshua tree and in some of the other plants. Additional slides were made from the same materials after triturating in order to bring the material into approximately the same condition as it occurs in the sloth dung. Both stained and unstained sections were prepared. In most cases balsam mounts were preferred, although glycerine and Farrant's medium were found to be more suitable in certain preparations.

In the case of the larger leaves, such as those from the yuccas and *Agave,* eight or more epidermal sections were taken from each leaf, since it was found that the cell pattern and disposition of the stomates varied with the different parts of the leaf. This point is one of considerable importance, since epidermis from the unexposed base of the *Yucca* or *Agave* leaves is very delicate and has few or no stomates, while that from the exposed parts is tough and parchment-like with numerous stomates. Tissue fragments of the delicate type might easily be mistaken for that of some hydrophilous plant unless a special study of this aspect of the subject has first been made.

While it is true in general, that the coarser desert vegetation has a tough, impervious epidermis, this does not apply in all cases. The epidermis of *Atriplex* (saltbush), for example, is very thin and tenuous. Protection from the too intense action of dry air and sunlight is obtained by means of inflated hairs which give the plant a highly reflecting surface and to which its silvery white color is due.

In a great many cases some preliminary treatment was necessary before the material could be prepared for sectioning. This included the use of solvents for removing the deposits of wax, oil or resins which coat many of the leaves. This is especially true in the case of *Larrea* (creosote bush). In this instance the leaves are coated with a layer of brown pigment and a shellac-like varnish. The plant required repeated treatments with acetone, which was found to be the appropriate solvent, before epidermal sections could be made.

MACROSCOPIC DESCRIPTION OF GROUND SLOTH DUNG

The large masses of ejecta are generally more or less flattened or discoidal in shape and average about 10 or 11 cms. in their largest dimension by about 5 or 6 cms. thick (see Plate 2). Most of these consist of single masses of material, but frequently several smaller balls have been pressed into a single laminated disk. The surface is commonly somewhat smooth and may be glossy with a hard brown coating of dried mucus varnish. The vegetable nature of their component material is apparent at once. The material is shown in Plate 2.

When one of the balls is broken, the interior is found to consist of a wadded mass of dried vegetable tissue, mostly fiber, with light yellowish to orange-colored fragments of the tough epidermis of some desert plant, which examination proves to be *Yucca* and *Agave.* The material seems to have been poorly masticated, since large pieces of the woody stems of such plants as *Atriplex* and *Ephedra,* up to 3.5 cm. long, are of common occurrence. The sharp tips of *Yucca brevifolia* and *Agave utahensis* also occur. The fragments of epidermis range in size from those small enough to pass through a 100-mesh sieve to fragments 2 cm. long. Many of the fragments show the serrated edges common to *Yucca brevifolia,* as Dr. Howard has remarked in his report.

In addition to the fibers and epidermis, parts of the flower stalk, seed pods and entire seeds also occur. In all cases where yucca seeds have been observed, these appear to be from *Yucca brevifolia.* The flat black testa has been split in each instance and all indication of the contents lost.

EXAMINATION OF THE MINUS TWENTY MESH FINES

When one of the dung balls is broken, much fine yellowish powder is liberated. Most of this will pass through a 100-mesh screen. The pieces which remain after this treatment are found to be mostly epidermis and fiber. In our examination of this fraction everything smaller than 20-mesh was examined as a whole without separating into finer fractions.

This fraction is very important and was made the subject of extensive examination. One of the striking features of this material is the great abundance of crystals, large prisms and bundles of raphides of calcium oxalate. Clusters and radiating groups of the same substance also occur. Chemical analyses of several samples of this fraction showed that fully 50 per cent of the powder consisted of calcium oxalate. Nearly all of the residue consisted of such substances as fiber, epidermis, hairs, stone cells and pollen.

Aside from the tissue fragments which were known to be from *Yucca* and *Agave,* much evidence of other genera was found. It is characteristic of many desert plants that they part with their epidermis with great difficulty. Even after prolonged maceration some of these may yield very small fragments.

Generally, as occurring in the dung, entire leaves have been crushed to a pulp, and microscopical examination shows only tiny fragments of the epidermis, some still attached to the palisade layer. The samples prepared by trituration were of value particularly in the identification of this material. Commonly, these smaller particles are obscured by a coating of brown resin, which, upon precipitation from solution, appears identical with the resin precipitated from *Larrea* by the same method.

After the acetone extraction, numerous pollen grains were uncovered. Pollen which appears identical with that from *Yucca, Bebbia, Œnothera, Sphæralcea, Typha* and from several other plants was abundant. Other types, which as yet have not been identified, were found. While the pollen grains appear identical with those of the species mentioned, both in form and in measurement (Plate 3), the writers do not wish to convey the impression that the identifications are positive, since the specimens may well be of other closely related types.

Plant hairs were abundant in this fraction and many of these allow of positive identification. An outstanding feature of some of the balls is the presence of spiked or tuberculated hairs of *Petalonyx* (sandpaper bush). These are very typical (Plate 9, figs. 7 and 8). Others were like those from *Bebbia, Aristida, Sphæralcea, Encelia* and *Tidestromia* (Plate 9). Some of the hairs were still attached to minute fragments of the epidermis. This is especially true of *Larrea;* the hairs and clumps of pigment cells were very evident. The sawtoothed margins and interlocking, crenate-edged cells of a grass, probably *Aristida,* were not uncommon.

A few scattered fibers from some coniferous wood, easily identified by the presence of bordered pits were found. This is most likely from *Juniperus utahensis* or *Pinus monophylla* (Plate 4), both of which grow abundantly at higher altitudes in the region of Gypsum Cave. *Ephedra,* although belonging to the gymnospermæ, does not show this characteristic (Plate 4).

The varying composition of the dung balls, aside from the presence of *Yucca,* which is always the chief constituent, is well shown by an examination of the fines. Some samples will exhibit much material of *Petalonyx,* while in other samples evidence of this genus may be entirely absent. This may indicate a difference in the feeding range from day to day or it may be seasonal.

It is remarkable that no spines of any of the cacti have been observed so far, since these plants are frequently eaten by range cattle in spite of the presence of spines.

Much unidentified material is present in nearly every sample (Plate 10). One fragment of *Yucca* with jigsawed serrations has not yet been identified. It may be shown later that the specimen is from very young leaves of *Yucca brevifolia.* Some of the unidentified detritus may consist of the ova of various insects and the excreta of the same organisms. It seems more likely that this material was ingested by the sloth while feeding, than that the substances were introduced after the dung was deposited in the cave.

IDENTIFICATION OF THE LARGER FRAGMENTS

Large pieces of epidermis were removed from the broken mass of ejecta after macerating in warm water. It may be remarked at this point, that this treatment produced a strong aromatic odor, which is typical of the strongly scented plants upon which the sloth fed. No animal odor was apparent. The large fragments were removed with a forceps and, as usual, treated with a weak solution of hydrochloric acid to remove the encrusting layer of calcium oxalate which was nearly always present. The sections were then stained and mounted, before subjecting them to examination. It was a rare occurrence for the large fragments to be other than those of the epidermis of *Yucca brevifolia* and *Agave,* although *Yucca baccata* and *Yucca mohavensis* were observed in a few cases (Plates 5 to 8). All the specimens from the sloth dung stained as readily as fresh material. This is remarkable when the probable age of the material is considered.

In general, the fibrous portion of the dung balls, with the exception of yucca fiber, defied identification. A few specimens of the twigs of *Ephedra,* showing the fibers with their typically spatulate ends, were found. In table 1, a list is given of all the plants collected both at Gypsum Cave and at the Clark Mountain locality. The righthand column indicates the species which were identified on the basis of material found in the dung balls.

DIFFERENCES IN PLANT ASSEMBLAGES OCCURRING IN DUNG OF GROUND SLOTH AND WILD BURRO

The writers believed that it might be significant to compare the plant tissues found in the sloth dung with that of an animal feeding on the same range today. The burro was selected since feral burros are common in the desert. The ejecta from these animals were collected near the cave and examined in the same way as were those of the ground sloth. *Yucca, Agave, Ephedra* and *Petalonyx* were entirely absent. *Atriplex* and grasses, including types which closely resemble *Aristida,* were abundant. Remains of *Sphæralcea* and other herbaceous plants were common. The burro material was more completely masticated than that from the sloth and seemed to be more completely digested, if the dissociation of the fibrous material into its component parts is to be considered as an indication. The difference in type between the coarse fibers of the yuccas and the more delicate fibers of the smaller plants is to be borne in mind.

CONCLUSIONS

All the foregoing evidence indicates that *Nothrotherium* was preeminently a yucca-feeder, while living in the vicinity of the cave. Other plants were eaten, but only secondary to the yuccas and plants of the same type. The presence of *Typha* (cat-tail) indicates that plants growing near water were eaten when available. *Yucca brevifolia* and *Agave utahensis* are not found near the cave at the present day, but are common in the Clark Mountains and other high localities where less arid conditions prevail.

With the exception of the yucca with jigsawed serrations, the plants so far identified are all of well-known types. There is every reason to believe that when one views today the vegetation of the Clark Mountains (Plate 11), one sees the same type of plant environment in which the ground sloth lived when it inhabited Gypsum Cave. In general, the plant assemblage represented in the sloth dung is found today only at elevations 3000 or more feet higher than Gypsum Cave. In other words, at the time when ground sloths, and perhaps man, inhabited Gypsum Cave, the climate was distinctly more humid than it is today. Whether that moister age was Pleistocene or Recent remains an open question.

TABLE 1—*Comparative list of plants from southern Nevada.*

Species	Gypsum Cave vicinity	Clark Mts.	Sloth dung flora
1. Pinus monophylla Torr.	..	X	?
2. Juniperus utahensis Lem.	..	X	X
3. Ephedra nevadensis Wats.	X	X	X
4. Typha sp.	..	..	X
5. Hilaria rigida (Thurb.) Benth.	X	..	..
6. Aristida reverchoni Vasey	X	..	X sp.
7. Yucca brevifolia Engelm.	..	X	X
8. Yucca baccata Torr.	..	X	X
9. Yucca mohavensis Sarg.	X	X	X
10. Agave utahensis Engelm.	..	X	X
11. Atriplex confertifolia Wats. (up to 6000 ft.)	X	..	X sp.
12. Tidestromia oblongifolia (Wats.) Standl.	X	..	..
13. Cowania stansburiana Torr.	..	X	..
14. Acacia greggii Gray	X	X	..
15. Krameria grayi Rose & Painter	X	..	..
16. Parosela johnsonii (Wats.) Vail	X	..	..
17. Larrea divaricata Cav.	X	X	X
18. Thamnosa montana Torr. & Frem.	X	..	..
19. Rhus trilobata Nutt.	..	X	..
20. Sphæralcea ambigua Gray	X	X	X
21. Petalonyx sp.	X	..	X
22. Œnothera multijuga Wats.	X	..	X sp.
23. Œnothera cæspitosa var. marginata (Nutt.) Munz	..	X	..
24. Menodora spinescens Gray	..	X	..
25. Coldenia canescens DC.	X	..	..
26. Lycium andersonii Gray	X	..	..
27. Nicotiana trigonophylla Dunal	X	..	..
28. Chilopsis linearis Gray	X	..	..
29. Aster abatus Blake	X	..	..
30. Bebbia juncea var. aspera Greene	X	..	..
31. Chrysothamnus speciosus Nutt.	..	X	X sp.
32. Encelia farinosa Gray	X	..	..
33. Franseria dumosa Gray	X	..	..
34. Hymenoclea salsola T. & G.	X	..	..
35. Peucephyllum Schottii Gray	X	..	..

The abbreviation sp., following the sign indicating the occurrence of a plant in the sloth dung, denotes the recognition of characters typical of the genus with, however, no positive determination of species.

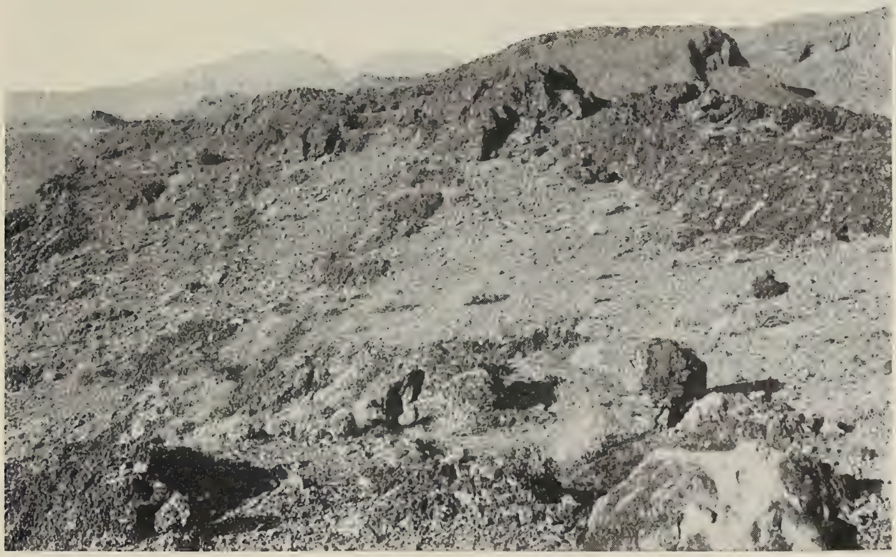


Fig. 1—View looking southwest from limestone ridge in which Gypsum Cave is located, showing presence of extremely scant vegetation. C.I.T. Photograph No. 651.

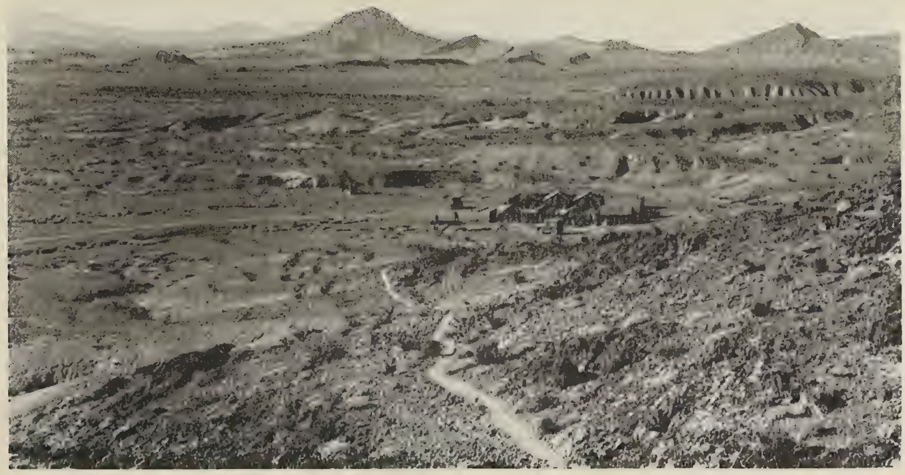
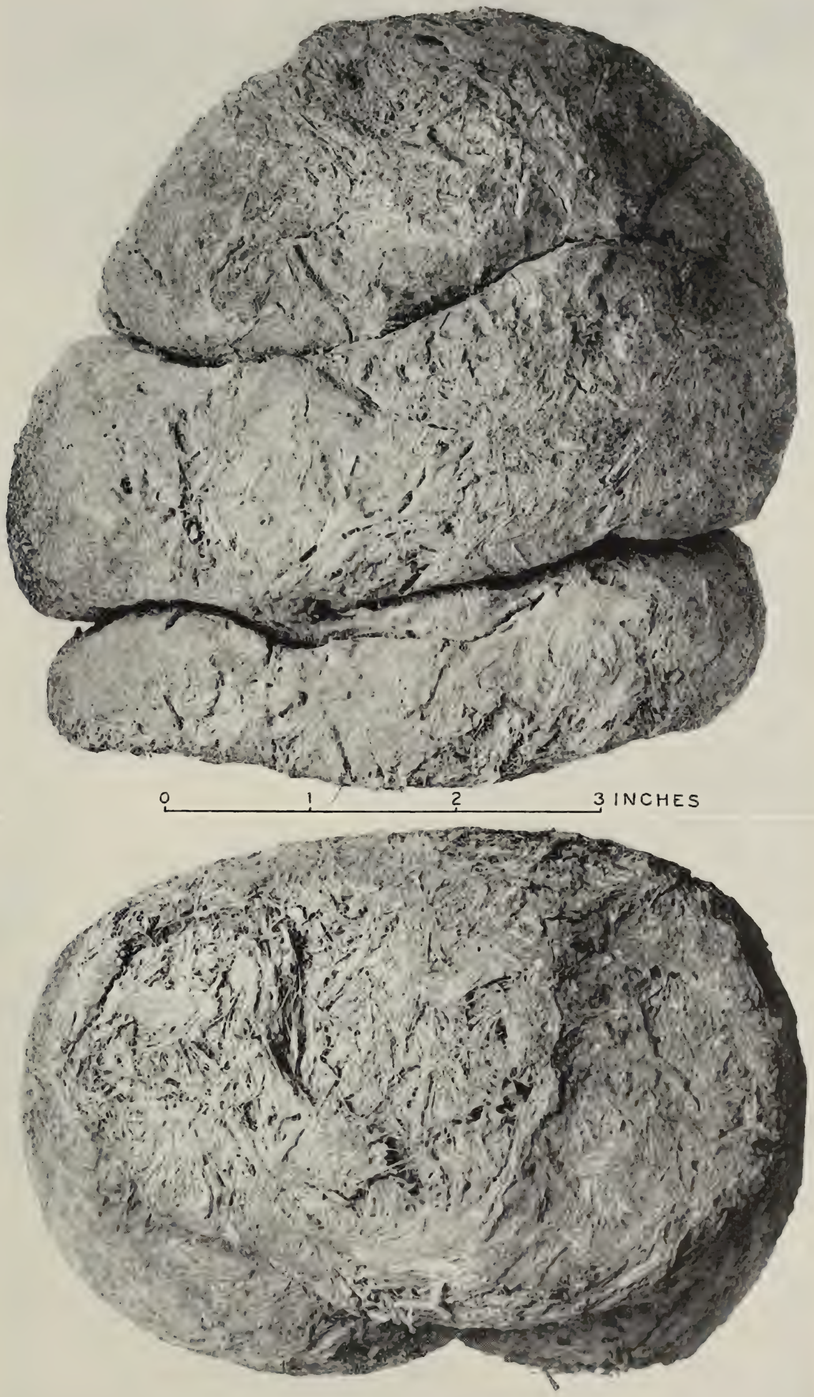


Fig. 2—View looking south from site of Gypsum Cave. Scattered clumps of dark brush are *Larrea.* C.I.T. Photograph No. 652.



Nothrotherium shastense Sinclair

Typical dung ball. Lower figure shows fibrous internal structure of dung.

Description of Plate 3

Fig. 1—*Larrea divaricata* Cav.

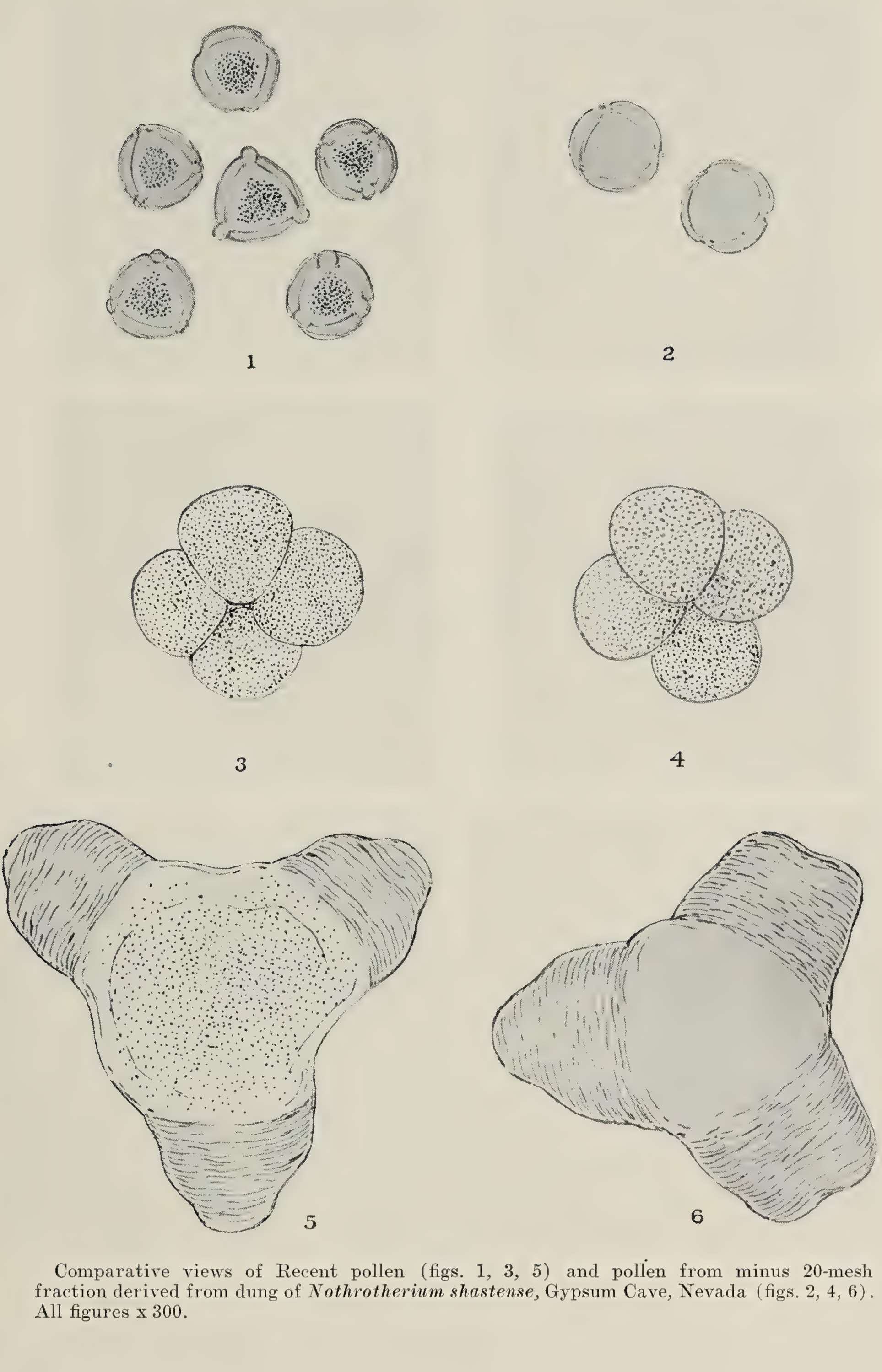
Fig. 2—*Larrea divaricata* Cav.?

Fig. 3—*Typha angustifolia* Linn.

Fig. 4—*Typha* sp.

Fig. 5—*Œnothera cœspitosa* var. *marginata* (Nutt.) Munz.

Fig. 6—*Œnothera* sp.



Comparative views of Recent pollen (figs. 1, 3, 5) and pollen from minus 20-mesh fraction derived from dung of *Nothrotherium shastense,* Gypsum Cave, Nevada (figs. 2, 4, 6). All figures x 300.

DESCRIPTION OF PLATE 4

FIG. 1—*Pinus monophylla* Torr. Fibers from young wood showing bordered pits; x 300.

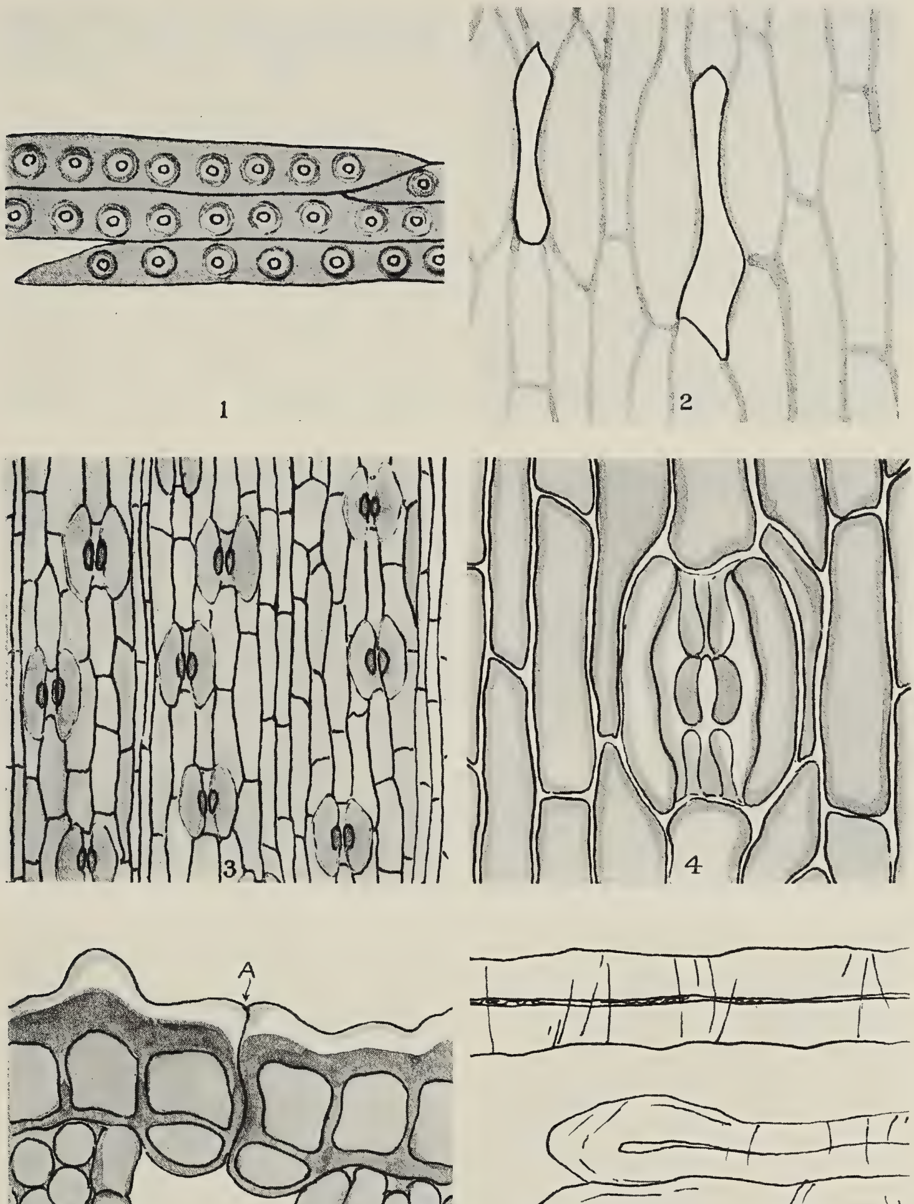
FIG. 2—*Ephedra nevadensis* Wats. Surface view of epidermis; x 300.

FIG. 3—*Ephedra*. First sub-surface view; x 75.

FIG. 4—*Ephedra*. A single stomate; x 300.

FIG. 5—*Ephedra*. Transverse section of epidermis. A stomate with closed guard cells is shown at A; x 300.

FIG. 6—*Ephedra*. Fibers staining violet with chloroiodide of zinc (cellulose). The spatulate ends of the fibers are typical; x 300.



Histological characters determined in Recent plant tissues. Where comparable structures have been identified in plant remains from the *Nothrotherium* dung, no figures of the latter material are included.

DESCRIPTION OF PLATE 5

FIG. 1—Surface view of outer layer of cells of the epidermis. The rounded ends of the cells with their disposal around a stomate rift are shown at right of figure; x 300.

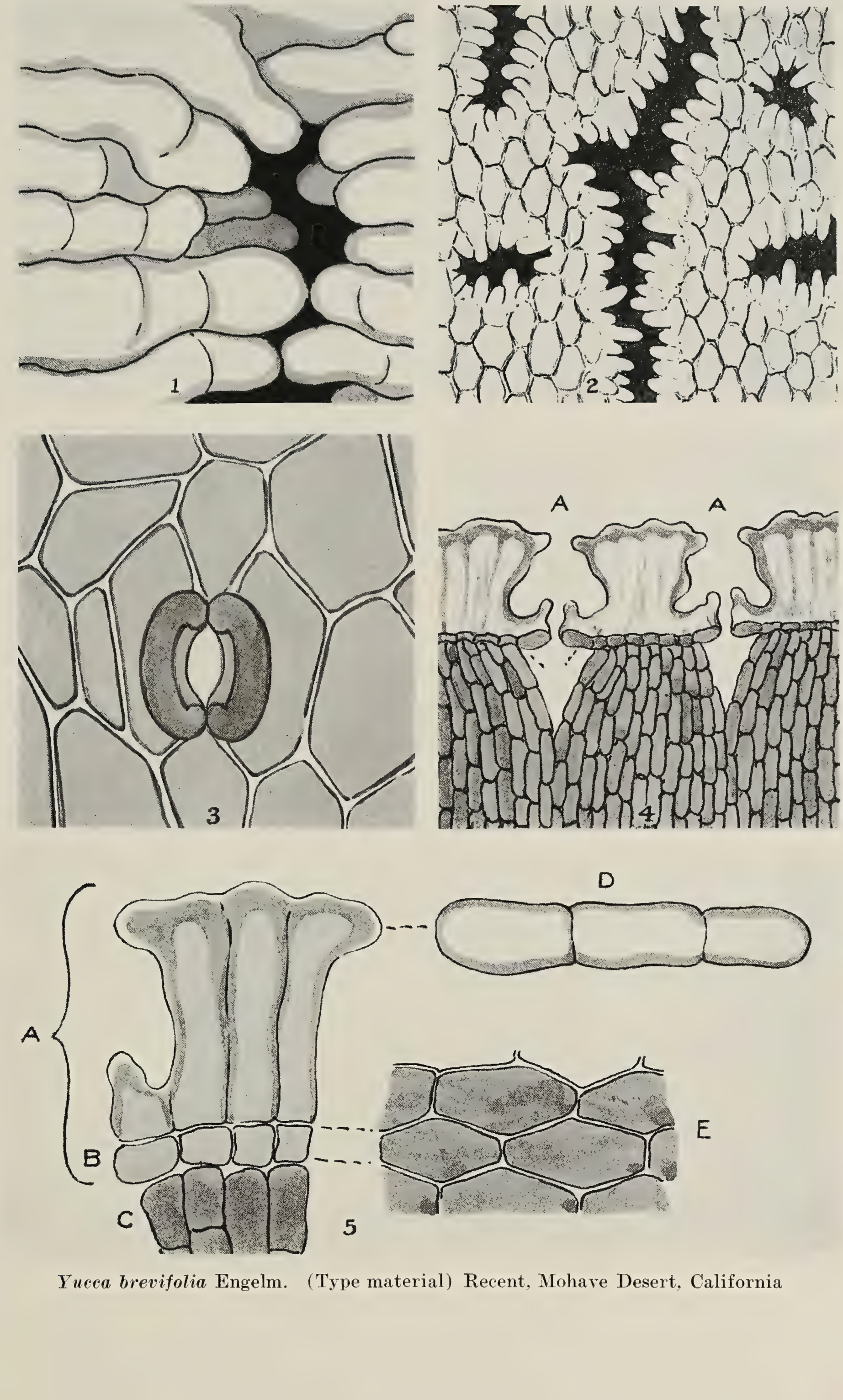
FIG. 2—First sub-surface view of epidermis showing reticulated cell pattern and modified epidermal cells bordering a stomate rift; x 75.

FIG. 3—A single stomate in association with cells of reticulated layer. In *Yucca brevifolia* and *Yucca mohavensis,* stomates lie in chainlike groups at bottoms of stomate rifts; x 300.

FIG. 4—Transverse section through epidermis and part of palisade layer. At A-A are shown profiles of two stomate rifts. Guard cells of a stomate are shown at B; x 75.

FIG. 5—Transverse section through four cells of the epidermis. At A is shown group of cells composing epidermis proper. This includes cells of reticulated layer indicated by B. A surface view of this group of cells is shown at D. At E are cells of reticulated layer whose ends, shown in profile, constitute the line of cells shown at B.

Layer A has an average thickness of from 80 to 100 microns; x 250.



Yucca brevifolia Engelm. (Type material) Recent, Mohave Desert, California

Description of Plate 6

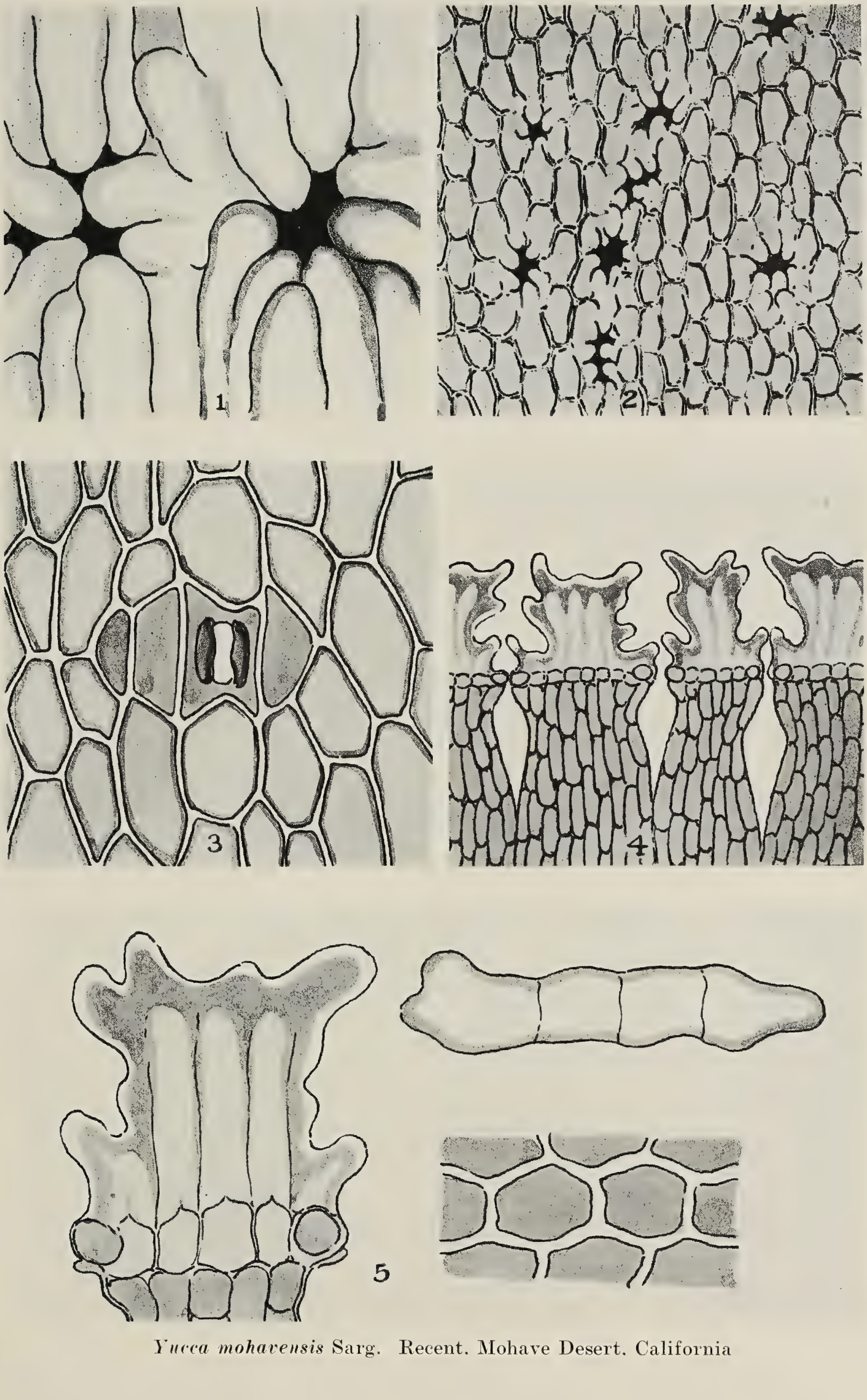
Fig. 1—Surface view of outer layer of cells of epidermis; x 300.

Fig. 2—First sub-surface view of epidermis. The tendency to form long rifts of stomates is not so pronounced in *Yucca mohavensis* as in *Yucca brevifolia,* but frequently occurs; x 75.

Fig. 3—A single stomate; x 300.

Fig. 4—Transverse section through epidermis; x 75.

Fig. 5—Transverse section through epidermis; x 250.



Yucca mohavensis Sarg. Recent. Mohave Desert. California

Description of Plate 7

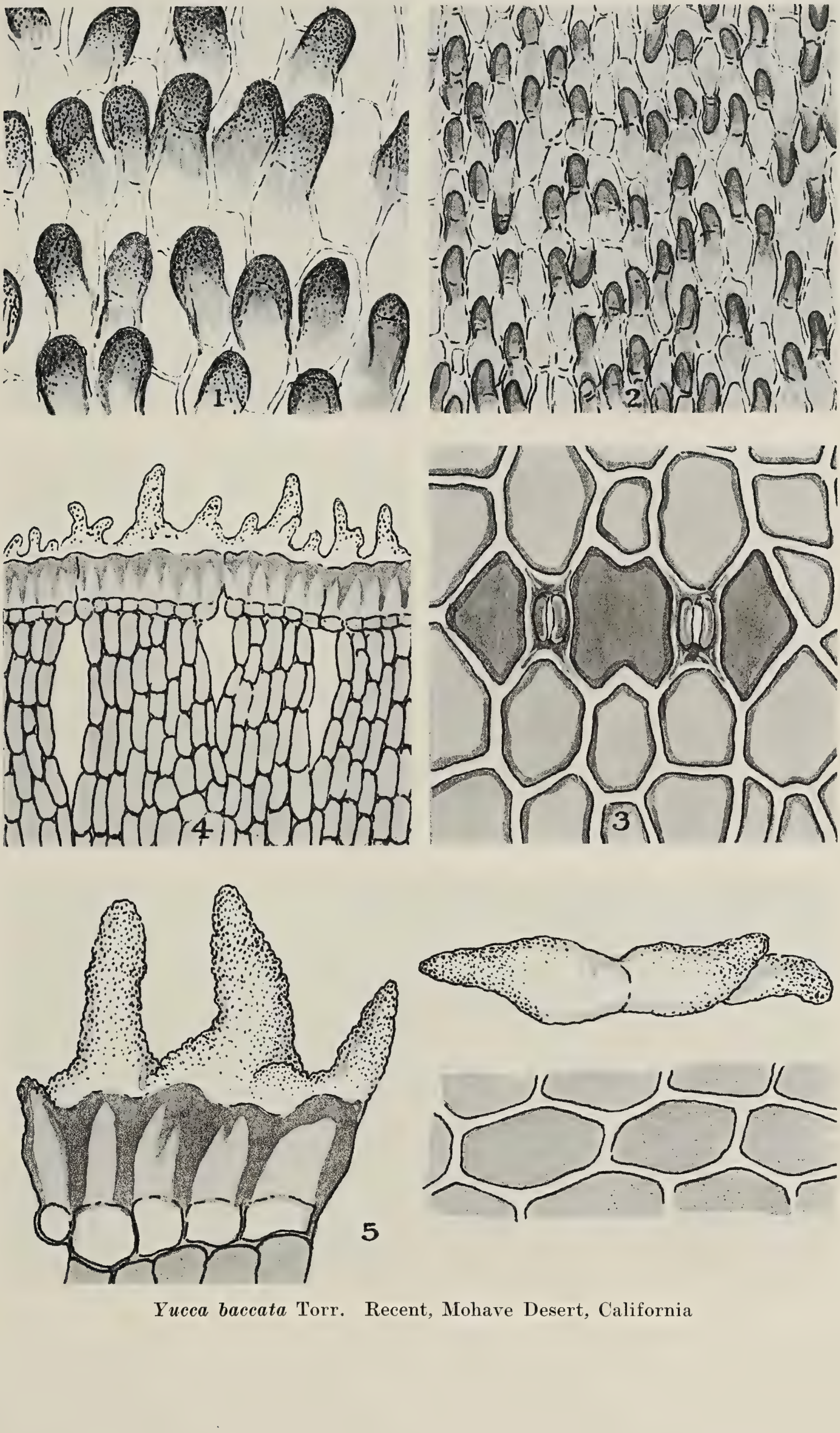
Fig. 1—Surface view of outer layer of cells of epidermis showing papillose surface of cells. This characteristic is a constant feature of *Yucca baccata;* x 300.

Fig. 2—Surface view of epidermis. Absence of stomate rifts is to be noted; x 75.

Fig. 3—First sub-surface view of epidermis. Conjoined stomates are common; x 300.

Fig. 4—Transverse section through epidermis. Relatively thin epidermis, absence of stomate rifts, and papillæ with their granular surfaces, indicated by stippling, are shown; x 75.

Fig. 5—Transverse section through cells of epidermis; x 250.



Yucca baccata Torr. Recent, Mohave Desert, California

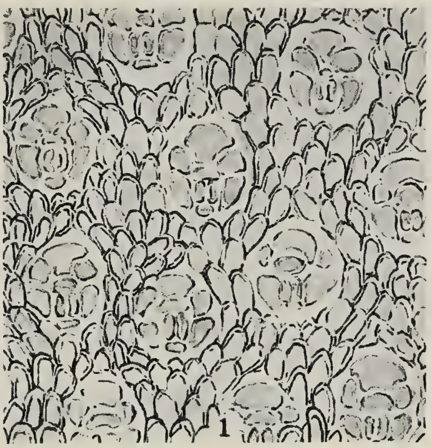
Description of Plate 8

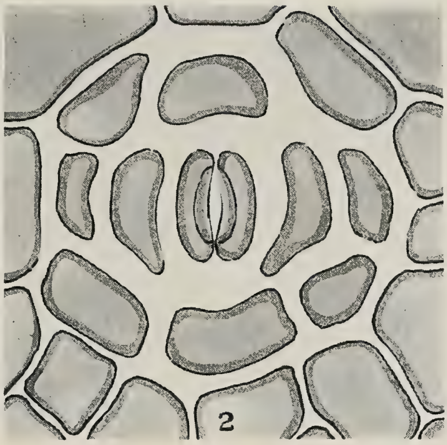
Fig. 1—Surface view of epidermis; x 75.

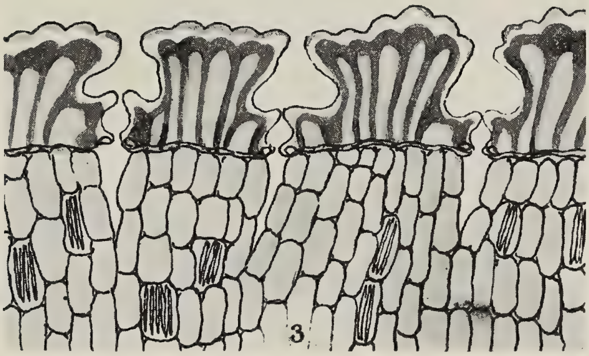
Fig. 2—First sub-surface view of a single stomate; x 300.

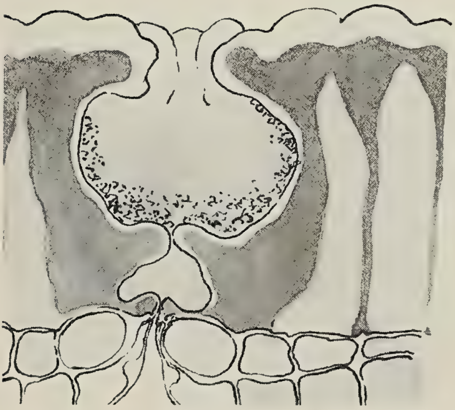
Fig. 3—Transverse section through epidermis; x 75.

Fig. 4—Transverse section through a stomate. The stomate vase commonly shows a granular deposit as indicated in the figure; x 250.









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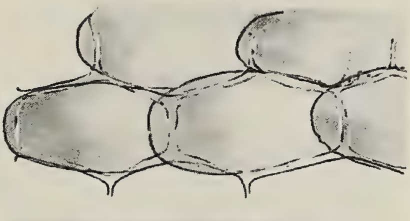


Agave utahensis Engelm. Recent, Mohave Desert, California

DESCRIPTION OF PLATE 9

Hair and epidermis of a grass (*Aristida* ?) from minus 20-mesh fraction from the dung of *Nothrotherium shastense* (figs. 2 and 4) compared with Recent material (figs. 1 and 3). The small bean-shaped knobs, which are common on grass fragments from the fines, are isotropic and have an index of refraction which is distinctly lower than that of the cellulose-like material lying beneath. The index is probably below that of balsam and the findings are not compatible with the view that they consist of opaline silica.

FIG. 1—*Sphæralcea ambigua* Gray. Stellate hair of leaf; x 240.

FIG. 2—*Sphæralcea?* x 300.

FIG. 3—*Aristida reverchoni* Vasey. Epidermis of stem; x 300.

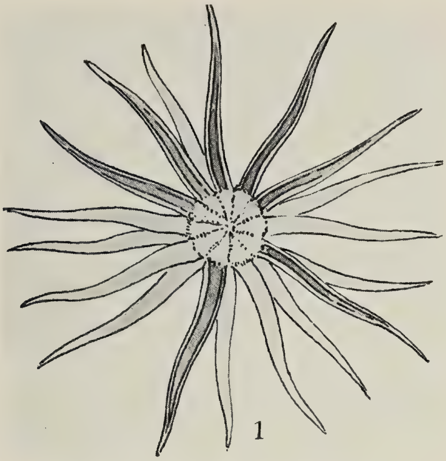
FIG. 4—Grass. Probably *Aristida;* x 300.

FIG. 5—*Yucca brevifolia* Engelm. Recent, Mohave Desert, California. A single serration; x 75.

FIG. 6—Unidentified yucca from minus 20-mesh fraction from the dung of *Nothrotherium.* Compare jigsawed serration with that of *Yucca brevifolia;* x 75.

FIG. 7—*Petalonyx nitidus* Wats. Recent, Mohave Desert, California. A single spiked hair. The slender, sharply pointed type shown and shorter, bluntly terminated hairs may occur on same leaf; x 250.

FIG. 8—*Petalonyx* sp. From minus 20-mesh fraction from dung of *Nothrotherium;* x 250.



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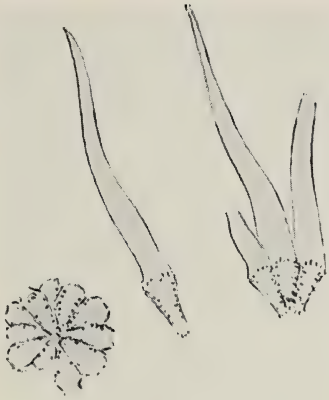

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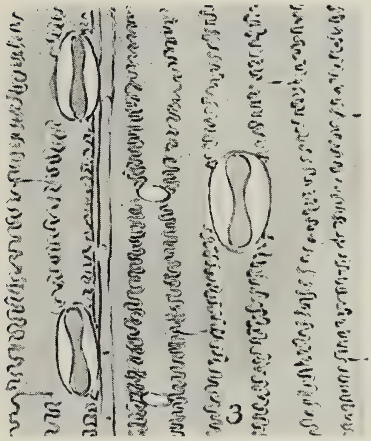

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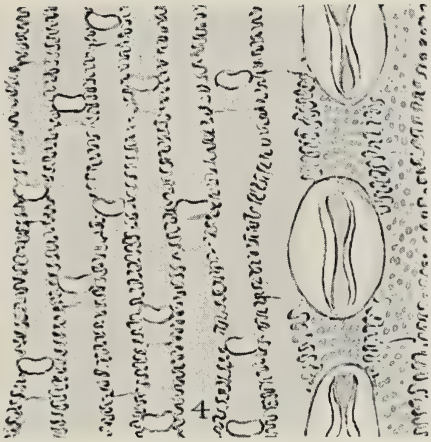

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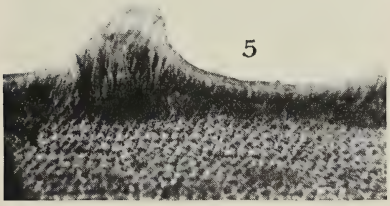

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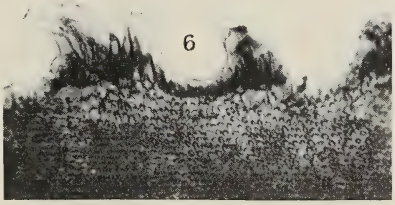

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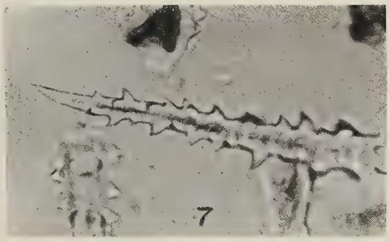

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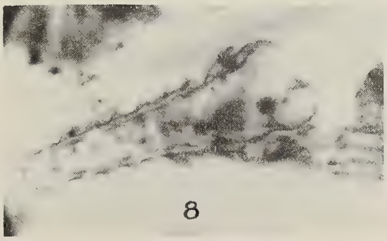

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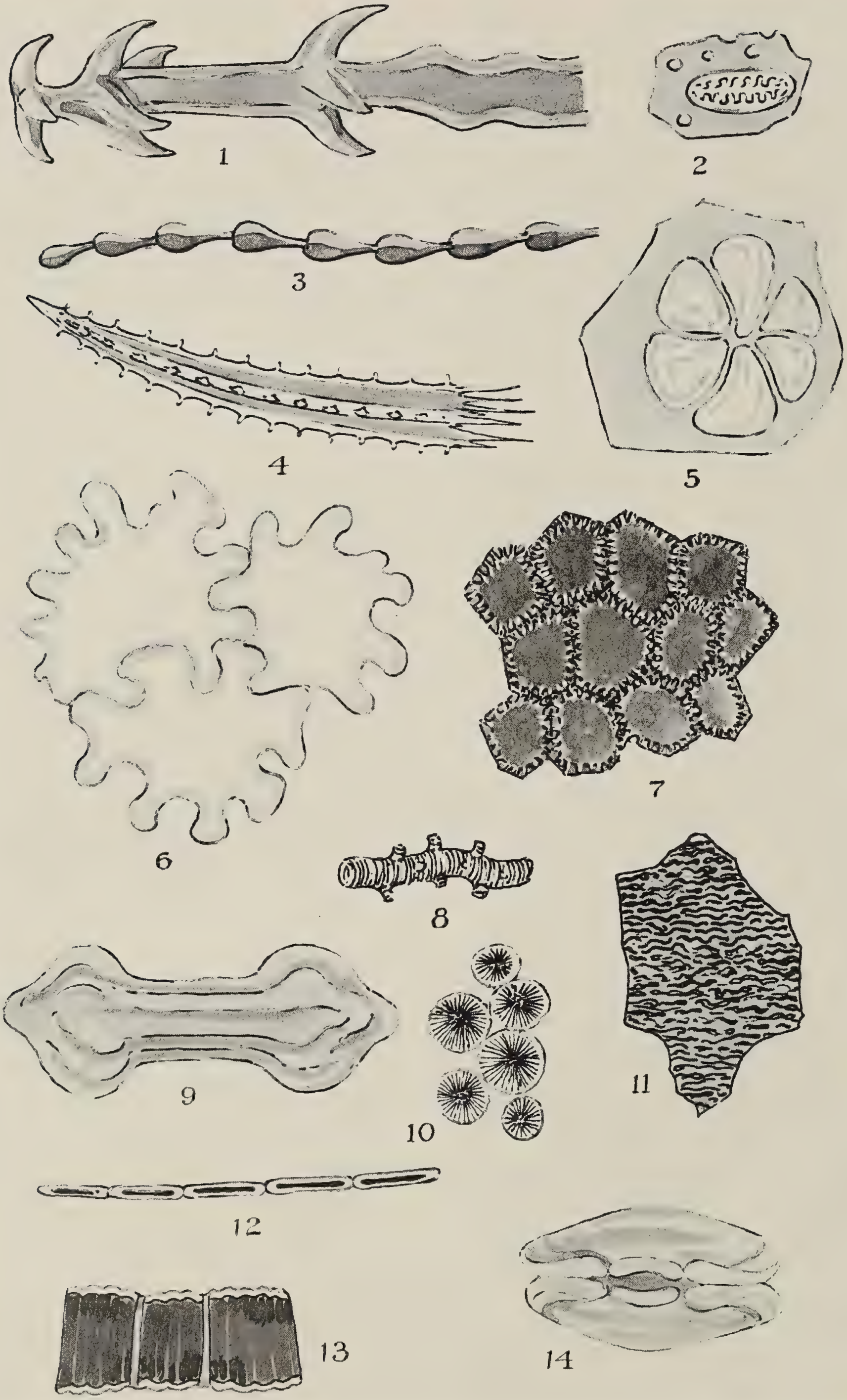
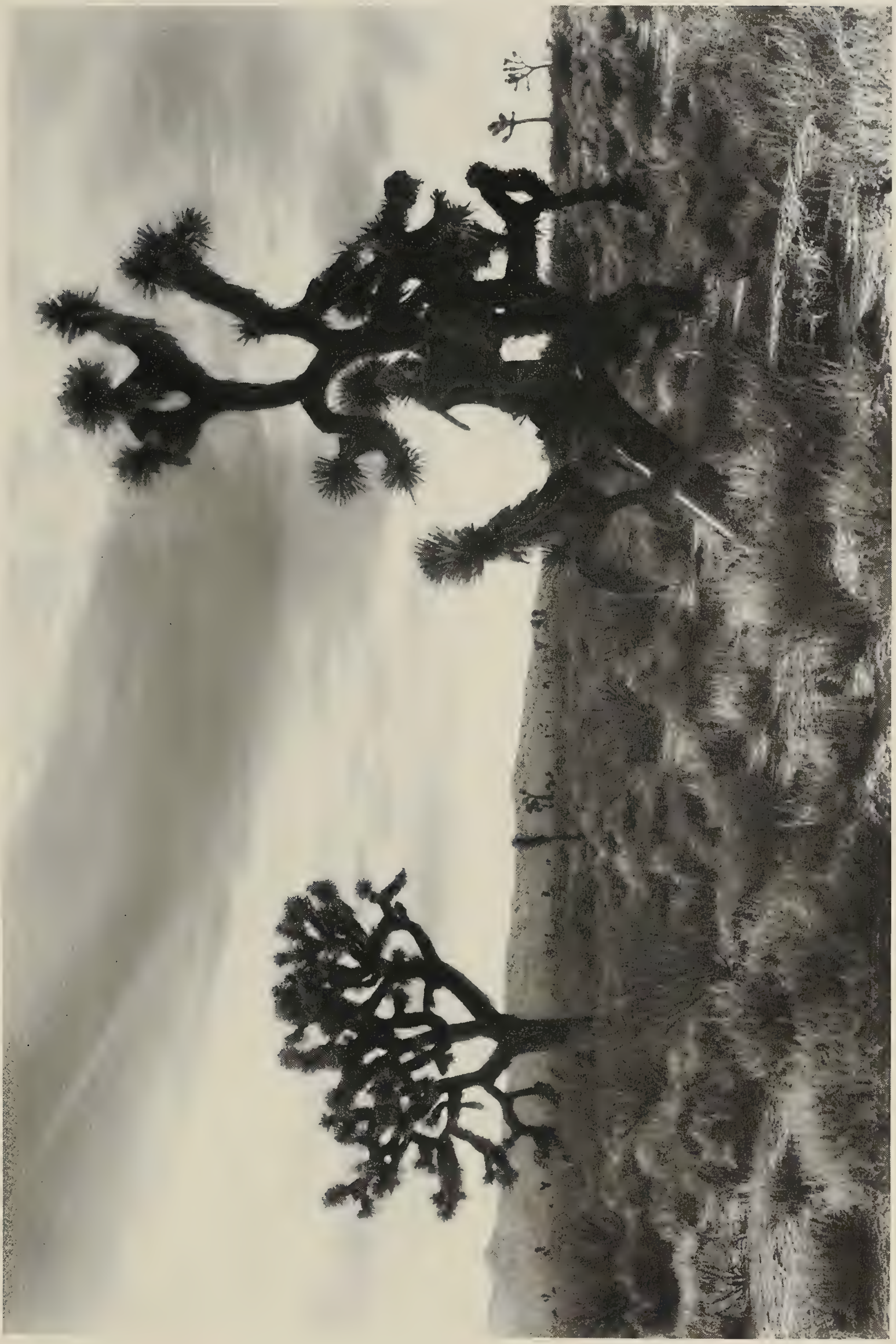


Unidentified material from minus 20-mesh fraction from dung of *Nothrotherium shastense*. Objects shown are of constant occurrence in this fraction, but their origin has not been determined; x 300.



View of a typical landscape in the Clark Mountains, California. The large branched trees with tufts of spiky leaves are *Yucca brevifolia*; low clumps of bush are principally *Ephedra*.

CONTRIBUTIONS TO PALÆONTOLOGY

V

TOOTH CHARACTERS OF PROTOHIPPINE HORSES WITH SPECIAL REFERENCE TO SPECIES FROM THE MERYCHIPPUS ZONE, CALIFORNIA

By Francis D. Bode

With two plates and six text-figures

[Issued December 20, 1934]

CONTENTS

Page

Introduction........ 41

Description of Material........ 42

  Merychippus brevidontus n. sp........ 42

  Merychippus californicus Merriam........ 43

Variation in Cheek-tooth Characters of Fossil Horses and its Stratigraphic Significance.. 47

    Superior Cheek-teeth........ 49

    Inferior Cheek-teeth........ 56

  Consideration of Single Characters........ 48

  Views of Other Authors........ 59

Conclusions........ 61

TOOTH CHARACTERS OF PROTOHIPPINE HORSES WITH SPECIAL REFERENCE TO SPECIES FROM THE MERYCHIPPUS ZONE, CALIFORNIA

INTRODUCTION

The critical review of equine tooth characters attempted in this paper is the result of a study of the protohippine horses obtained from the Merychippus Zone of the north Coalinga district, California. During the conduct of extensive excavations in this zone since 1928 by the California Institute, more than two thousand teeth of the genus *Merychippus* have been collected. In addition to the types represented by the equine material, a number of associated land mammals have been secured. The faunal list, which includes some fifteen species, suggests that this locality occupies a stratigraphic position approximately late middle Miocene in age.

The variation displayed in the dental characters of the merychippine material from the Merychippus Zone necessitated comparisons with cheek-teeth of Equidæ from practically all of the Miocene formations furnishing vertebrate remains in the Pacific Coast and Great Basin Provinces. A comprehensive study of these collections clearly demonstrates that many of the cheek-tooth characters employed in the description of type specimens of fossil horses are variable to an extent which renders them unreliable in a determination of species. The variation of these characters within a large collection also indicates that it is possible for teeth referable to a particular species to have a wider stratigraphic range than has been hitherto appreciated. The conclusion is reached that the presence of a species has less value in reaching an age determination of the strata in which it occurs than evidence furnished by an association of several species.

Indebtedness is acknowledged to the Museum of Paleontology, University of California, for a generous loan of fossil material, including type specimens, from the Barstow and Mascall formations. The writer takes this opportunity to thank Dr. Chester Stock for advice given during the course of the investigation. The illustrations have been prepared by John L. Ridgway. The enamel patterns of cheek-teeth reproduced in the text were accurately outlined on photographs of the specimens. The photographic prints were then treated in a bleaching solution, which obliterated the photograph but did not affect the ink outline.

DESCRIPTION OF MATERIAL

Merychippus brevidontus n. sp.

Type specimen—P$\underline{3}$, No. 1414, Calif. Inst. Tech. Coll., Merychippus Zone, north Coalinga district, California. (Plate 1, figs. 3-3b.)

Paratypes—P$\underline{4}$, No. 1413; M$\underline{2}$, No. 1408; M$\underline{1}$, No. 1422; Calif. Inst. Tech. Coll., Merychippus Zone, north Coalinga district, California. (Plate 1, figs. 6-8.)

Referred specimens—Series of upper and lower cheek-teeth, Nos. 1409-1412, 1415-1421, 1423-1432, Calif. Inst. Tech. Coll., Merychippus Zone, north Coalinga district, California. (Plate 1, figs. 4-4b, 5-5b, and Plate 2, figs. 4-12.)

Specific characters—Crowns of cheek-teeth fully hypsodont but extremely short relative to size of cross-sections. Enamel pattern of upper and lower cheek-teeth highly complex with complexity continuing almost to base of crown.

This species is represented in the collections by approximately seventy-five upper and lower cheek-teeth. The species is found also in formations of middle Miocene age at Virgin Valley, Nevada, and Skull Spring, eastern Oregon.

The principal character is the great complexity of the enamel pattern, associated with fully hypsodont but relatively short crowns. In unworn teeth the average height of crown is 20.5 mm. The maximum measurement was 23.4 mm. and the minimum 18.7. The cross-sectional area is comparable in size to that seen in the type of *Merychippus isonesus* Cope. As many as seventeen enamel folds have been observed on the borders of the fossettes. The pli-caballin is sometimes tripartite, is never absent and rarely single. At the juncture of the protoloph and the metacone, the prefossette is sometimes incompletely enclosed on relatively unworn teeth. In such instances the lingual end of the protoconule shows a curious increase in number and in arrangement of plications. The protocone usually possesses a spur extending toward the protoconule. The hypocone is flattened and elongate. The long axis of this cusp is oriented usually in an anteroposterior direction. The cusp is often twice as long as the protocone and is frequently not connected with the metaconule.

The average height of crown of the inferior cheek-teeth is 21.3 mm. The number and type of plications of the enamel walls are unique for a tooth of this size, the complexity frequently approaching that seen in lower teeth referred to *Hipparion mohavense* Merriam. The metaconid-metastylid column usually occupies well over one-third of the anteroposterior width of the crown and remains separate throughout the wear of the tooth. The entoconid extends far across the lingual valley and frequently touches the metaconid. The internal walls of the protoconid and hypoconid usually carry several plate-like projections or crenulations of enamel. The teeth are well cemented.

The type of *Merychippus sphenodus* Cope presents a similar type of enamel pattern, but exhibits a much higher crown. *M. brevidontus* differs from *M. severus* Cope (fig. 2, e to i) in complexity of the enamel pattern, shortness of crown and in larger cross-sectional area of crown. Teeth of *M. severus* are considerably higher crowned. The type of *M. relictus* Cope is also smaller in cross-section than in the Californian form and the enamel pattern is characterized by its simplicity. Moreover, unworn teeth referable to *M. relictus* (fig. 2b and 2d) have a height of crown comparable to that in *M. isonesus* Cope. *M. westoni* Simpson and *M. gunteri* Simpson approach the small Coalinga species in shortness of crown. However, the teeth in the Florida species seem to possess a much simpler enamel pattern. *M. brevidontus* is distinguished from *M. isonesus* (fig. 3a to 3m) by its shorter crown and more complex enamel pattern. In his description of the Miocene horses from the Sheep

Creek and lower Snake Creek horizons of western Nebraska, Matthew [1] refers to a collection of very short-crowned teeth. Although not certain of their affinities, Matthew regarded them as belonging to a form distinct from the *M. paniensis* group. Nearly all of these specimens are unworn teeth and a comparison of the enamel pattern with that of *M. brevidontus* is consequently difficult. The size of crown comes close to that of *M. brevidontus.* It is possible that these forms are sufficiently similar as to be specifically related. It is interesting to note that, as in the case of the large collection from the north Coalinga horizon, those from the Sheep Creek and lower Snake Creek horizons contain, along with a large number of normal-sized teeth of *Merychippus,* a few very short-crowned teeth whose characters do not grade into the larger and highly variable group. It may be mentioned that up to the present time these small forms have always been found in association with a progressive species of *Parahippus.*

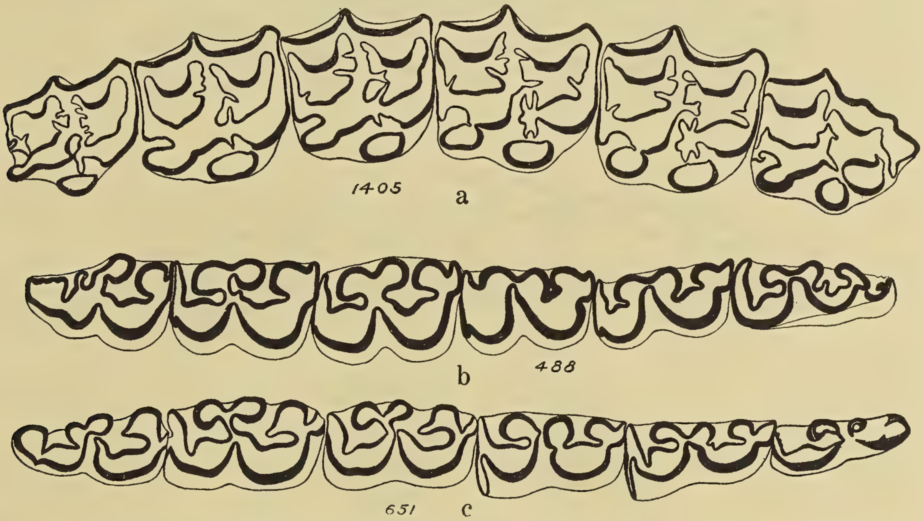


FIG. 1—*Merychippus californicus* Merriam. Referred specimens. a, composite upper cheek-tooth series, No. 1405; b, c, individual lower cheek-tooth series, Nos. 488 and 651; x 1. Calif. Inst. Tech. Coll., Merychippus Zone, California. (Specimens show average grouping of characters seen in teeth from the Merychippus Zone.)

Merychippus californicus Merriam

Type specimen—M$\underline{1}$, No. 21247, Univ. Calif. Coll. Vert. Pale., Merychippus Zone, north Coalinga district, California.

Referred specimens—A composite series of upper cheek-teeth, P$\underline{2}$-M$\underline{3}$, No. 1405; mandibles with all cheek-teeth present, Nos. 488 and 651, Calif. Inst. Tech. Coll., Merychippus Zone, north Coalinga district, California. (Fig. 1-1c.)

The material from the Merychippus Zone consists almost entirely of scattered teeth and fragments of limb elements. In the entire collection no associated upper cheek-teeth are present. Three more or less complete mandibles were collected during the progress of the excavations. The limb bones have suffered considerably from abrasion, presumably during transportation in water. Skeletal materials are so fragmentary and are usually so well worn that they possess little taxonomic value.

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[1] W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 50, 159, 1924.

The amount of variation (figs. 3 to 6) seen in over two thousand teeth referable to this species makes it impossible to find any one character sufficiently unique to afford a constant distinction between *Merychippus californicus* and many of the specific forms belonging to this genus. Some of the teeth in the collection are specifically inseparable from specimens of *M. sumani* Merriam (fig. 5) from the Barstow. Others can not be distinguished from the type of *M. isonesus* (figs. 3 and 4). In like manner, selections can be made of teeth whose characters approach those of most of the described species of *Merychippus*. Only when the collection is regarded as a whole can differences be recognized.

For the superior dentition, referred specimen No. 1405 (fig. 1a) Calif. Inst. Tech. Coll. is seen to be considerably more typical of the group than is the

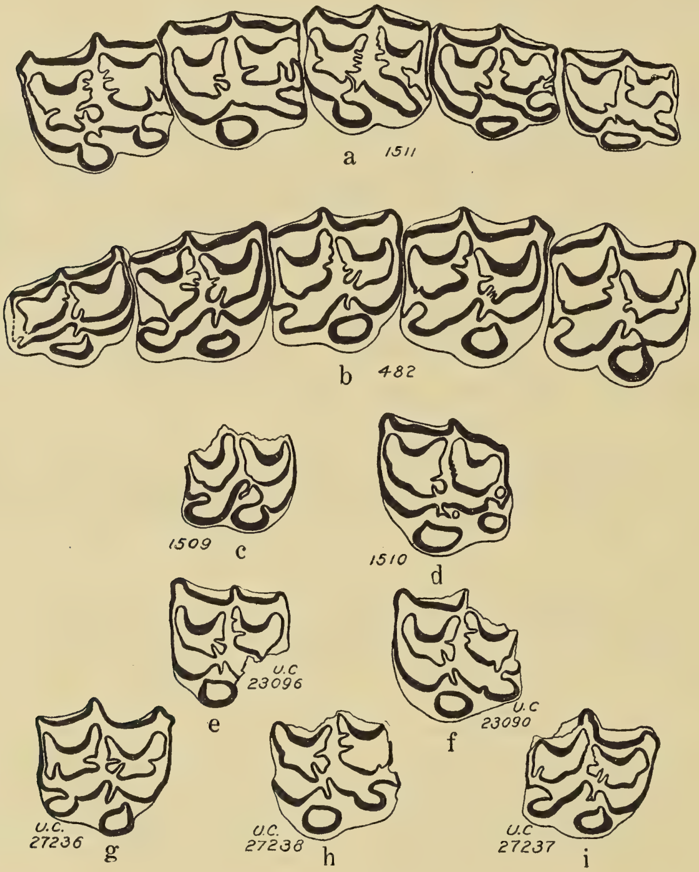

FIG. 2—a, ***Merychippus primus*** Matthew, composite upper cheek-tooth series of referred specimens showing extent of variation of enamel patterns, Sheep Creek middle Miocene, western Nebraska. b, ***Merychippus relictus*** (Cope), referred specimen, upper cheek-tooth series of one individual shows type of pattern of small teeth that may be referred to this species, Skull Spring middle Miocene, eastern Oregon. c, d, ***Merychippus relictus*** (Cope), referred specimens, Skull Spring middle Miocene, eastern Oregon. e to i, ***Merychippus seversus*** (Cope), referred specimens showing types of variation of enamel pattern of small teeth referable to this species. Mascall middle Miocene, eastern Oregon; x 1. (Specimen numbers designated "U. C." from Univ. Calif. Coll.; without designation, from Calif. Inst. Tech. Coll.)

type specimen described by Merriam.[1] However, it should be noted that some of the *Merychippus* teeth in the collections of the University of California from the Barstow Miocene, closely approach No. 1405. As is shown in this specimen, the union of protoconule with metaloph, to enclose the prefossette, is incompletely established in the premolars, and the lingual end of the protoconule is greatly plicated. These characters are present in approximately 70 per cent of all premolars of *M. californicus* from the Merychippus Zone, whose crowns have been less than half removed by wear. The prefossette is nearly always found completely enclosed in well-worn premolars and is always so in molars. Frequency of occurrence of an open prefossette in the premolars is apparently the most distinctive character found in the permanent teeth from the Merychippus Zone. It should be noted, however, that an open prefossette has been observed in a number of equine species and genera, among which may be mentioned: Specimens referred to *M. isonesus* from the Skull Spring locality in eastern Oregon; *M. sumani* and *M. intermontanus* from the Barstow; *Hipparion mohavense* and *Pliohippus tantalus* from the Ricardo of the Mojave Desert; and in at least five additional species found in the Great Plains region. The relatively small collections at hand from the several localities mentioned above make it impossible to determine accurately the incidence of occurrence of this character in these species. The material studied seems to indicate that the number of specimens with open prefossette is proportionately less. However, this character must be used with caution when employed in the identification of a merychippine species.

The lower cheek-teeth from the Merychippus Zone, exclusive of those referred to *M. brevidontus,* present no characters which serve to distinguish them from comparable teeth of most species of *Merychippus.*

The deciduous teeth of *Merychippus californicus* possess characters of greater taxonomic value than those of the permanent dentition (Plate 2, figs. 1 to 3). Compared to *M. isonesus* and similar species, the superior milk teeth in *M. californicus* are higher crowned, well cemented and the protocone and hypocone are cylindrical rather than conical. The hypocone is oriented with principal axis in an anteroposterior direction rather than in a diagonal direction, as seen in the Mascall species. The crescents are well developed and the fossettes completely formed, so that the Coalinga milk teeth resemble those of the permanent dentition. In *M. isonesus,* the deciduous premolars have a "*Parahippus*-like" appearance. The principal difference between the teeth from the Merychippus Zone and those from the Barstow is largely one of size, the latter being as a rule considerably larger. In size alone, the Coalinga specimens are more nearly comparable to those of *M. isonesus,* while the milk teeth from the Barstow are similar to corresponding teeth of *Protohippus.*

The inferior milk teeth from the Merychippus Zone are sometimes more than twice as high-crowned as average specimens from the Mascall. These teeth carry a thin deposit of cement along the lingual side. The external valley is well filled with cement. Compared to corresponding teeth from the Barstow, the Coalinga specimens are smaller, shorter crowned, but equally as well cemented.

It may appear from the foregoing description that the specific status of *Merychippus californicus* is questioned. Since some of the teeth are similar in character to the type of *M. isonesus,* it might be concluded that the Coalinga horse represents that species. On the other hand, an equal number

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[1] J. C. Merriam, Trans. Amer. Philos. Soc., n. s., vol. 22, pt. 3, 9, 1915.

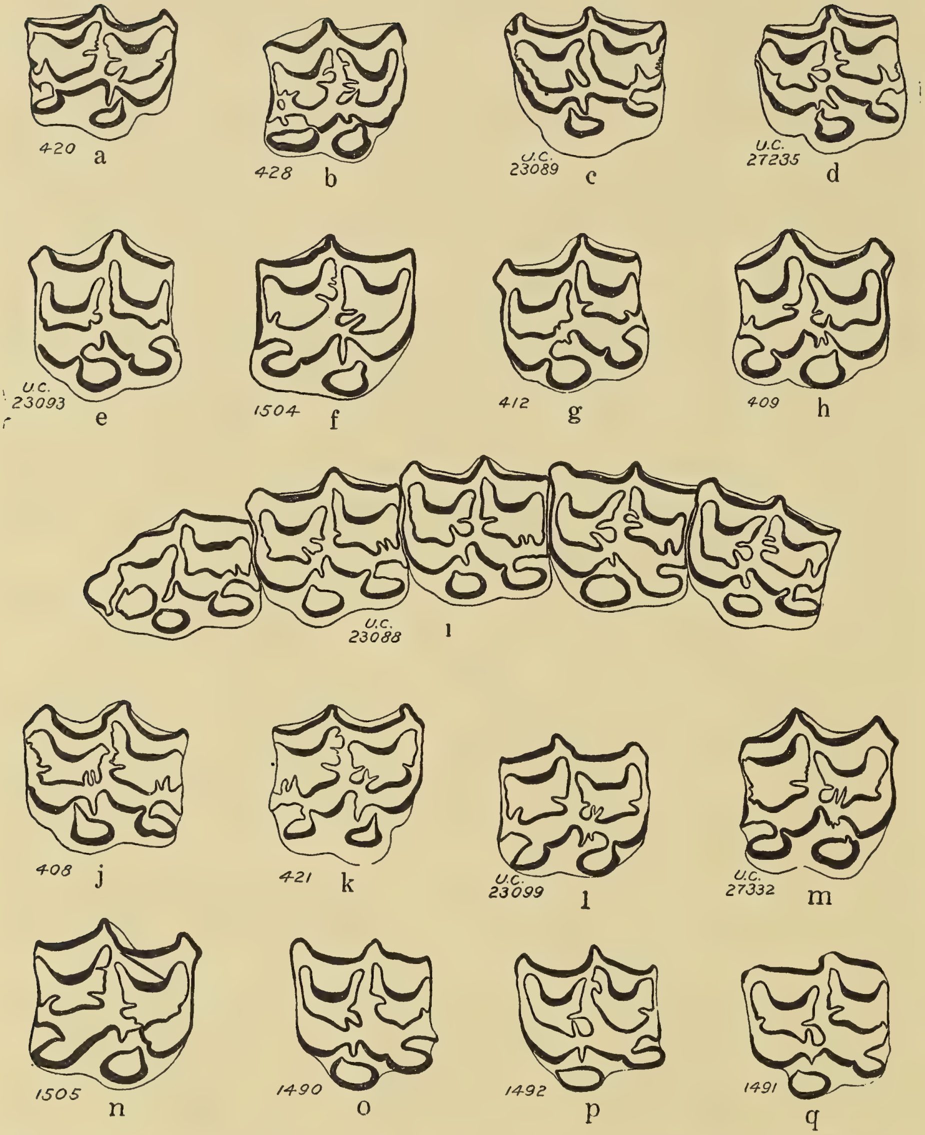

FIG. 3—a to m, *Merychippus isonesus* (Cope), referred specimens from Mascall middle Miocene of eastern Oregon showing some types of variation of enamel pattern; n to q, *Merychippus californicus* Merriam, referred specimens from Merychippus Zone showing types of enamel patterns similar to *M. isonesus;* x 1. (Specimen numbers designated "U. C." from Univ. Calif. Coll.; without designation, from Calif. Inst. Tech. Coll.)

of teeth from the Merychippus Zone have characters which approach those of the type of *M. sumani*. Specimens are available which approximate those of additional species belonging to *Merychippus*. Arbitrary assignment of the entire group to a described species other than *M. californicus* involves a procedure of little or no value, since such reference may be made with equal right to any one of a number of types. On the other hand, the collection may well be regarded as comprising teeth of several distinct, merychippine species. Were such a view adopted, however, a number of teeth would of necessity be recognized as possessing intermediate structural features and could consequently be regarded as characteristic of additional specific types. Rather than adopt a procedure which would become extremely unwieldy, it appears more desirable to retain within the *Merychippus californicus* group all these variant forms, with the referred specimen, No. 1405 (fig. 1a), presenting the average grouping of characters seen in teeth from the north Coalinga Zone. The latter is distinct from all other type specimens of merychippine species. No. 1405 may be regarded as typifying in its characters the species *Merychippus californicus*.

VARIATION IN CHEEK-TOOTH CHARACTERS OF FOSSIL HORSES AND ITS STRATIGRAPHIC SIGNIFICANCE

Since characters of the teeth of fossil horses are of considerable importance, not only in a determination of species but also in making a determination of the stratigraphic position of fossil material, it is important to acquire information concerning the variation and reliability of dental characters in these forms. The material from the Merychippus Zone offers opportunity to study the variation of cheek-tooth characters as exhibited in a large number of individuals, all referable to a single species. An attempt has been made, therefore, to determine the extent to which each character varies and to indicate the limits within which these characters can be safely used in their application to stratigraphy.

The collections from the Merychippus Zone were obtained at Locality 108, Calif. Inst. Tech. Vert. Pale., in a zone of sandstones and conglomerates approximately three feet in thickness. Deposition of the sedimentary beds probably required a relatively short period of geologic time. The fossil remains represent presumably a cross-section of the Equidæ, as this group existed during the unit of time recorded in the accumulation of the deposits of the Merychippus Zone. The small amount of time which elapsed during this deposition makes the possibility rather remote that the variation in tooth characters is due to progressive evolutionary changes within this merychippine species. Actual counts made of particular teeth in the cheek-tooth series indicate the presence of nearly two hundred individuals in the collections.

In approaching the study, a list was compiled of the cheek-tooth characters used by all known authors in describing species of the Equidæ with hypsodont teeth. This list shows that attempts have been made to employ more than fifty different peculiarities of tooth structure in the definition of species. The variation of each of these characters and its relation to the variation of all other characters was then observed in more than two thousand teeth from locality 108. In addition, comparisons were made with teeth from practically all Tertiary vertebrate horizons of the Pacific Coast and Great Basin Provinces.

It is not the purpose in the following discussion to invalidate a large number of described equine species. Nor is the account to be construed as an attempt to destroy the value of horse teeth as stratigraphic markers. Rather is it to be regarded as an effort to point out the degree to which characters of teeth of fossil horses vary, and to suggest methods by which such characters can be more accurately and reliably defined for stratigraphic purposes, especially with reference to the limits within which geologic age assignments may be made.

CONSIDERATION OF SINGLE CHARACTERS

As previously demonstrated by Gidley,[1] the factors responsible for differences in the enamel pattern of cheek-teeth may be divided into two groups: (1) Stage of wear of an individual tooth, and (2) individual variation.

As a single tooth is worn to the base of the crown, various changes in the enamel pattern and in the diametral ratios take place. The maximum complexity of the enamel pattern occurs when approximately the first one-fifth of the crown has been removed by wear. From this stage onward the complication of the enamel folds gradually decreases, the simplest pattern appearing at the base of the crown. The enamel pattern in both superior and inferior cheek-teeth, whose crowns have been worn almost to the base, is very simple. In such instances, it is practically impossible to reach more than an approximate determination of the type. Where the evolutionary stage represented by such a tooth is transitional between two genera, an assignment to either genus is questionable.

The maximum anteroposterior diameter in all cheek-teeth is situated near the summit of the crown in an unworn tooth. This diameter decreases gradually with wear. The transverse diameter gradually increases toward the base, usually becoming greater than the anteroposterior diameter in well-worn teeth. Ratios involving the use of these two diameters change materially with age. It follows therefore that the diameters and proportional ratios of a molar-premolar series may also vary with age. A large number of observations seems to indicate that the rate of change of these diameters and ratios is variable. Consequently, comparisons based upon these characters have little value. For purposes of comparison, only teeth that have attained the same stage of wear should be used and comparisons should be limited preferably to teeth in early stages of wear. In the following discussion of the variation of cheek-tooth characters, observations have been limited to teeth whose crowns have been less than one-third removed by wear.

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[1] J. W. Gidley, Bull. Amer. Mus. Nat. Hist., vol. 14, art. 9, 1901.

Among the numerous cheek-tooth characters employed by various authors, it appears especially desirable to discuss the following points.

SUPERIOR CHEEK-TEETH

Protocone—The shape, orientation and position of the protocone have been frequently used as specific characters. In the collections from the Merychippus Zone this cusp, while usually separate to the base of the crown, may also be found connected with the protoconule at any stage of wear. The cusp may be round or greatly flattened. When elliptical in cross-section, the orientation of the long axis may be in any direction. A spur or process extending toward the protoconule varies in size and is frequently absent. The enamel wall of this cusp is seen to be either inflated or indented. Its position with reference to other parts of the occlusal surface is variable. In addition, all characters vary with the wear of the tooth. In *Merychippus,* as in succeeding genera, separation of the protocone seems to be linked with the complexity of the enamel pattern. A protocone connected with protoconule at an early stage of wear is to be found more often in teeth whose enamel pattern is simple. A discrete protocone, on the other hand, is frequently found associated with more complex types of enamel patterns. This association exists throughout the geologic history of the genus *Merychippus* and appears to indicate that the major tooth characters, which distinguish *Hipparion* and *Pliohippus,* were foreshadowed long before the period when these genera appeared. A discrete protocone is of value in distinguishing *Hipparion* from *Pliohippus* or *Protohippus.* Its use in separating a primitive *Hipparion* from a progressive merychippine form, whose characters are approaching those of the former genus is of no value. A spur on the protocone is more characteristic of *Merychippus* than of *Hipparion,* but this character must be used with caution, since it has been observed in a few teeth referred to *Hipparion* and is frequently absent in *Merychippus.* Moreover, in those merychippine forms regarded as ancestral to *Hipparion,* and in *Hipparion* as well, a progressive tendency is noted toward enlargement of protocone in an anteroposterior direction and development of this cusp at the expense of the hypocone. Consequently, the latter cusp is displaced more and more toward the rear of the tooth. While the protocone may be employed on occasion to distinguish *Merychippus* and *Hipparion,* the numerous exceptions which have been noted obviate the possibility of general application.

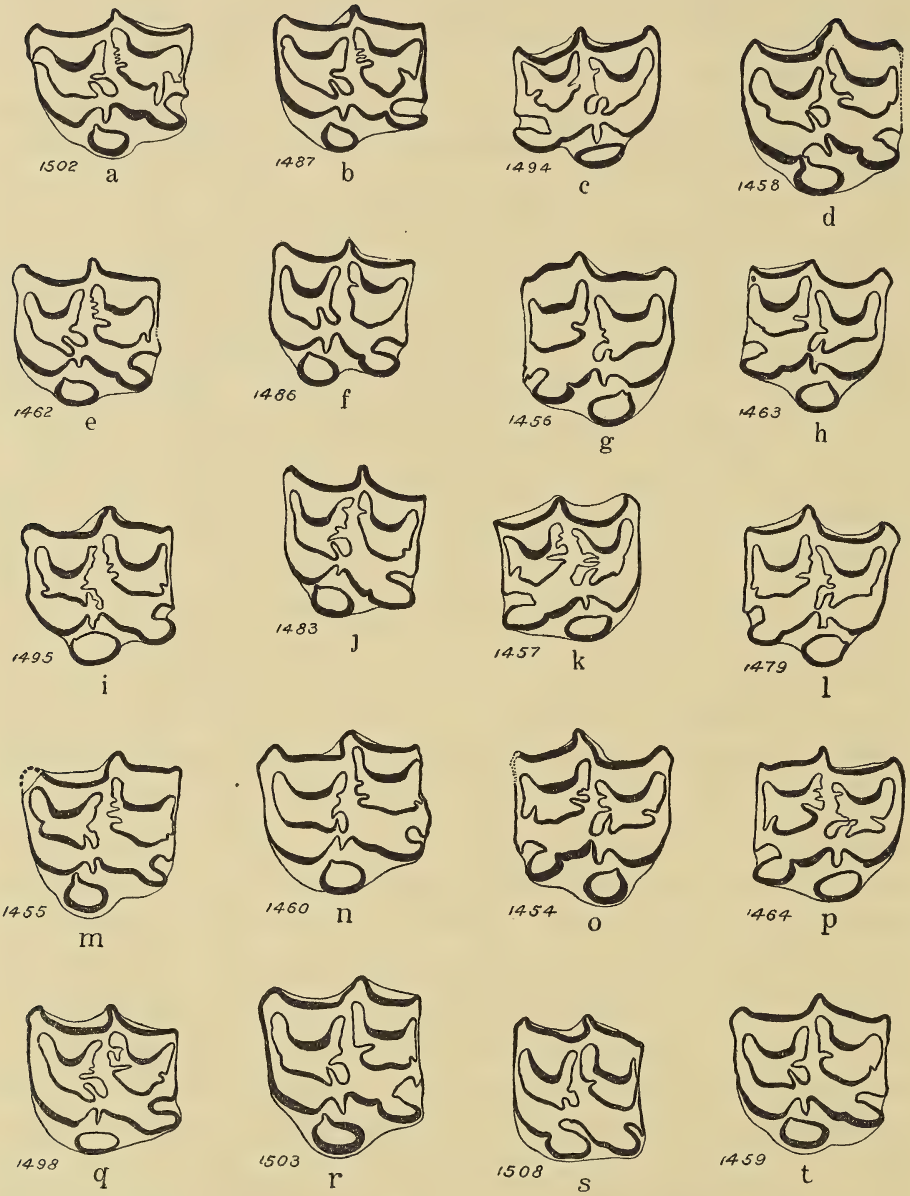

FIG. 4—*Merychippus californicus* Merriam. a to t, referred specimens showing variations of enamel patterns similar to *M. isonesus;* x 1. Calif. Inst. Tech. Coll., Merychippus Zone, California.

In *Protohippus* and in *Pliohippus* the protocone is always connected with the protoloph. In *Protohippus* the protocone is nearly equal to the hypocone in size and is sometimes connected with that cusp. The distinction between *Protohippus* and *Merychippus* as based on this cusp is usually fairly well marked; although in species situated near the border line between the two genera, the distinction is by no means so clearly defined. In *Pliohippus* the protocone also tends to become larger, but unlike that in *Hipparion* this cusp remains connected with the protoloph and develops progressively toward the anterior side of the tooth. The forward extension of the protocone on the anterior side of the isthmus clearly distinguishes *Equus* from *Pliohippus.* A study of material referable to *Plesippus* indicates that the use of the characters of this cusp in the definition of the latter genus is open to question.

The protocone presents by far the most characteristic structure of the occlusal surface. In fact, cheek-tooth characters of most of the genera are built around this cusp. While it is of great value in distinguishing the major lines of evolution in the Equidæ, its variations, as exhibited by the collection from the Merychippus Zone and by those from other Tertiary localities, are quite diverse within individual genera. Its use as a specific character is negligible and its value from the standpoint of stratigraphy is limited to two time stages for each genus, in that the progressive and primitive forms of a genus may be distinguished by the modification of the protocone. In intermediate stages the extent of variation would probably always include types comparable to the end stages as well.

Hypocone—In the material from north Coalinga, the hypocone is seen to vary in much the same manner as the protocone. It is sometimes found separate from the metaloph at a late stage of wear. It assumes a variety of shapes from round to flat. The position of the hypocone, relative to the other cusps, varies to a noticeable degree. In size, this cusp is usually, though not always, smaller than the protocone. The relative size of these two cusps is of little value as a distinctive character, however, since the hypocone is usually smaller than the protocone throughout the history of the Equidæ. In *Hipparion* the hypocone is pushed backward with development of the protocone. With the exception of the modification of the cusp in this genus, no evolutionary changes of stratigraphic value seem to have occurred.

Hypostyle and Pli-Caballin—These features of the occlusal surface are merely reflections of the complication of the enamel pattern. In a tooth in which the enamel pattern is simple, the pli-caballin is single or absent. Intricate enamel patterns are associated with a pli-caballin, which may be double or tri-partite. In like manner, the number of plications in the area designated as the hypostyle seems to be a func-

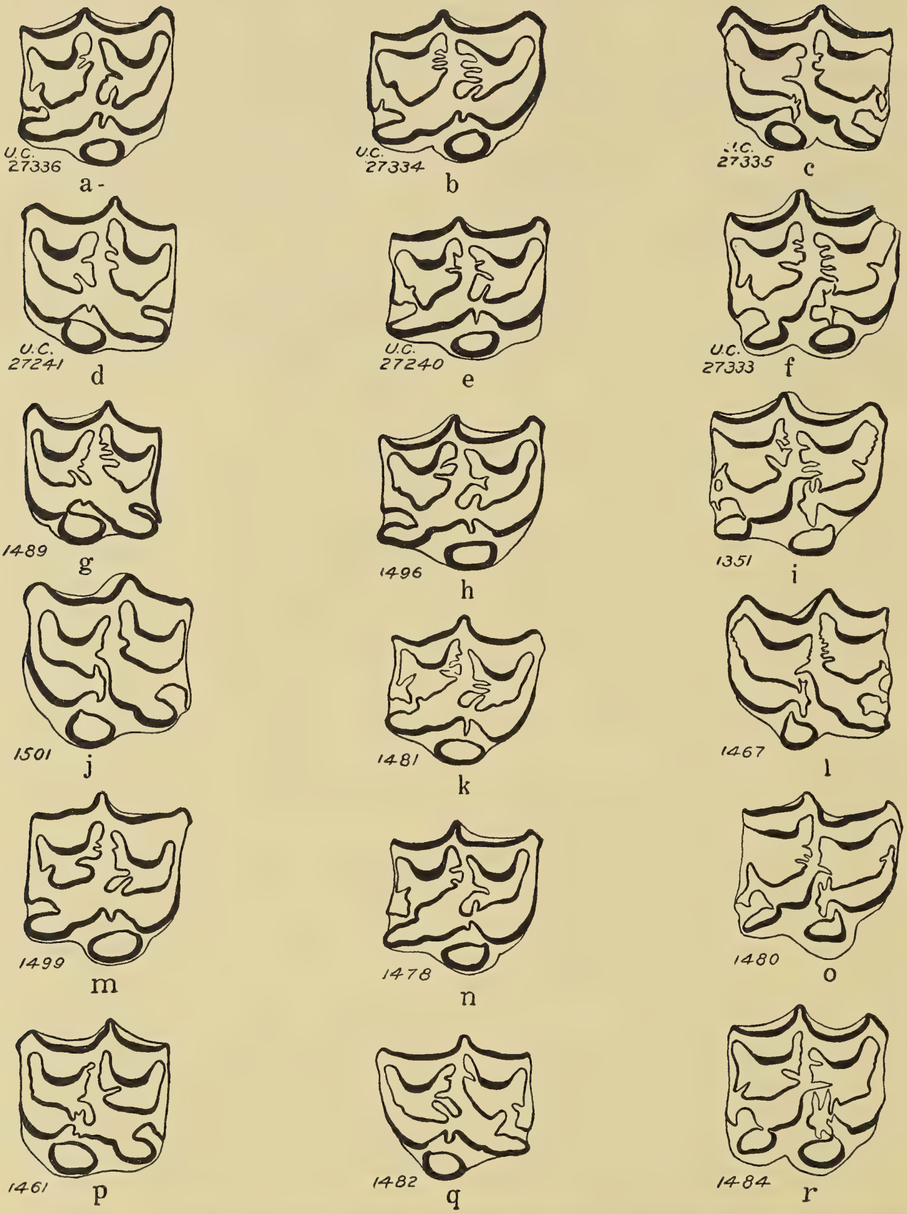

FIG. 5—a to f, *Merychippus sumani* Merriam, referred specimens showing examples of variation of enamel pattern. Univ. Calif. Coll., Barstow upper Miocene, California; g to r, *Merychippus californicus* Merriam, referred specimens showing types of enamel patterns similar to *M. sumani;* x 1. Calif. Inst. Tech. Coll., Merychippus Zone, California.

tion of the intricacies of the enamel walls of the fossettes. Considered alone, these characters have little value in the distinction of a species. They may be regarded as of same importance as the complication of the enamel walls of the fossettes.

Fossettes—Expansion or contraction of the fossettes and position of the external lobes has been found to be so variable in the materials studied as to suggest that these characters are completely unreliable for diagnostic purposes. Degree of complexity of the enamel walls of the fossettes appears to possess some general value. Such terms as highly, moderately or simply plicated borders are satisfactory when the description is based on the average grouping of occlusal characters as seen in a large group of specimens. Complexity of the enamel, when described in this manner, along with height and curvature of crown and appearance of protocone, furnish features of value in assigning specimens to their respective species. Complexity of the fossette borders is of value only if the crown is not too greatly worn. Moreover, comparisons of individual peculiarities are of no value since the number, shape and arrangement of the plications of the enamel walls are subject to a wide range of variation. In *Hipparion* the enamel pattern varies from moderately to highly complex. Some of the patterns exhibited by teeth referred to *Equus* may also show considerable complexity. In *Pliohipus* and in *Protohippus* the types of patterns are moderate to simple. All three stages of complexity are found in *Merychippus.*

External Styles—The strength of the external styles as displayed in teeth of a particular species is variable. Ratios indicating the relation of width of these styles to anteroposterior diameter of the entire tooth have been obtained for Tertiary horses from several horizons. These ratios and their range of variation were found to be similar in every collection furnishing materials for measurements. The strength of the styles, in relation to size of tooth, remains approximately the same in all genera.

Cement—An examination of teeth from numerous localities, representing stratigraphic stages from middle Miocene to Recent, indicates that the amount of cement present on a tooth has little value, even as a generic character for horses with hypsodont teeth. Some of the merychippine teeth from the Mascall carry as much cement in proportion to their size as do the large teeth of *Equus.*

Shape of Occlusal Surface—This is an unreliable character. As has been stated before, this surface is usually elongated in anteroposterior direction in relatively unworn teeth, and in worn teeth the greatest width is usually in transverse direction. The surface in moderately worn teeth is nearly square, but the shape varies considerably with the individual and with age. The variation of this character in teeth, which have reached practically the same stage of wear, is also considerable. A quantitative idea of this variation may be obtained from the ratios of the anteroposterior diameters to the transverse diameters. This ratio was calculated for more than three hundred first and second molars from the Merychippus Zone. The amount of wear to which each of these teeth had been subjected is approximately the same. The ratio varies from 1.40 to 0.85 and is sufficient to include most of the members of the Equidæ. Measurements of the last two premolars indicate that the shape of the occlusal surface in these teeth varies in a manner identical with that of the molars. The shape of M$\underline{3}$ and P$\underline{2}$ varies in still greater measure. This character has sometimes been used for specific distinctions. The variation is not due to extreme differences in anteroposterior diameters of the teeth, when compared to the rest of the series. Position of these teeth in the maxillary is variable and is rarely parallel to that of other cheek-teeth in an anteroposterior-vertical plane. Consequently, the occlusal surface is worn obliquely to the vertical axis of the tooth and the area of the surface is thus subject to a greater range of variation than that of intermediate teeth, whose position in the maxillary is more nearly constant.

Curvature of Crown—The extent of curvature of the crown is of value in distinguishing genera. Comparison of this character should be limited to unworn or slightly worn teeth. The original curvature can not be determined accurately for a tooth that has been more than half worn. In *Merychippus,* as indicated by the collections studied, the crowns of cheek-teeth are curved to varying degrees and are rarely straight. In *Hipparion* the teeth are straight to only slightly curved. This character is of particular value in distinguishing primitive forms of *Hipparion* from progressive types of *Merychippus* which possess teeth that are otherwise similar. However, caution must be exercised, for teeth from large collections of merychippine materials are sometimes, though infrequently, straight. In *Protohippus* and in the earlier forms of *Pliohippus* the crowns are curved. Greatest curvature of crown is seen in some species of *Pliohippus.* This character possesses no special value in distinguishing these two genera from *Merychippus.* Advanced forms of *Pliohippus* may not always be distinguishable from *Plesippus* and *Equus* by this single character.

Transverse Diameter—In observations on the value of tooth characters, Gidley[1] pointed out that following the early stages of wear the transverse diameter was only slightly variable. This opinion is somewhat substantiated by measurements made on teeth from the Merychippus Zone. The range in width as measured in millimeters is from 19.6 to 14.2, a difference of 5.4. However, it should be pointed out that most of the species of *Merychippus* fall within these limits. In addition, some teeth referred to *Parahippus, Protohippus, Pliohippus* and *Hipparion* give similar diameters. While the variation as measured in millimeters is not particularly large, the increase in this diameter during the evolution of the later equines was so gradual and slight as to render this character of little distinctive value as a time indicator.

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[1] J. W. Gidley, *op. cit.,* 105-106, 1901.

Height of Crown—Measurements of the height of crown of unworn teeth were made on more than five hundred specimens from the Merychippus Zone. Similar measurements were made also on teeth refer-

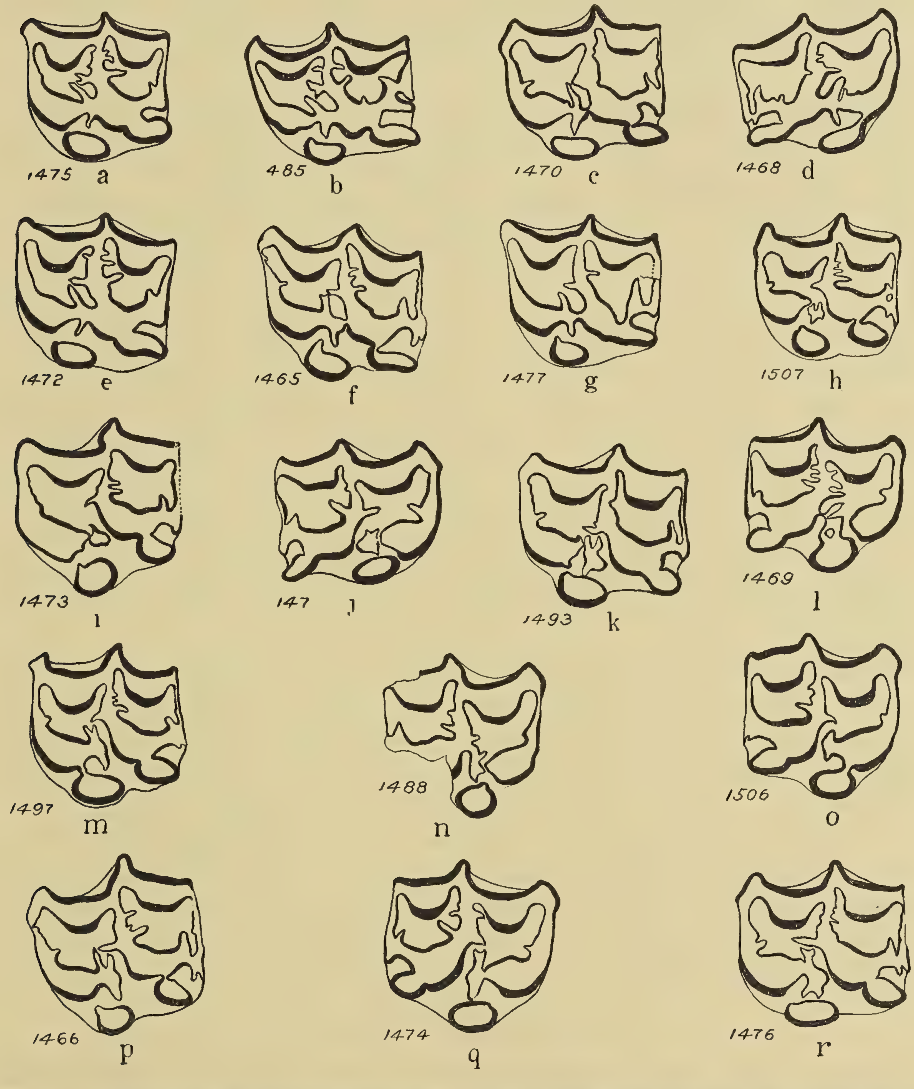

FIG. 6—***Merychippus californicus*** Merriam. a to r, referred specimens showing examples of variation of enamel patterns; x 1. Calif. Inst. Tech. Coll., Merychippus Zone, California.

able to *Merychippus isonesus* from the Mascall and Skull Spring localities in eastern Oregon, *M. sumani* and *M. intermontanus* from the Barstow, and on teeth of a merychippine form from an upper Miocene locality near Tonopah, Nevada. The following table gives the results of these measurements in centimeters.

Horizon	Species	Maximum	Mean	Minimum
Mascall	*M. isonesus*	3.4	2.9	2.6
Coalinga	*M. californicus*	4.2	3.4	2.9
Barstow	*M. sumani* and *M. intermontanus*	4.6	3.6	3.2
Tonopah	*Merychippus*, sp.	4.7	3.8	3.3

These results were obtained from measurements made on all superior cheek-teeth. Teeth from each position in the maxillary were represented in approximately equal numbers. Similar tables for teeth from each position vary through slightly different though equally discernible limits. A table showing averages for the entire series of cheek-teeth is considered more representative of the group. The results indicate that from middle to upper Miocene time there occurred a mean increase in height of crown of 9 mm. and that this measurement on teeth from any one locality varies considerably more than this. However, when, as in the present instance, large collections are available on which measurements can be based, a slight though definite increase in values can be demonstrated. The age evidence as afforded by the entire fauna from each locality is in accord with the stratigraphic arrangement given in the table. If the above four horizons are shown in future to be more closely grouped in the Miocene than is at present regarded to be the case, this character may be considered as increasing in value.

Character of height of crown is perhaps of great value in the recognition of species for stratigraphic purposes. No other character in teeth of the Equidæ seems to be quite so uni-directional in its trend. However, the values are pertinent only when a large collection of material is available. The height of crown in a few specimens or in an individual tooth has a stratigraphic value which is quite definitely less. The accuracy of this measurement, when obtained from a large collection, is limited by the time required for an appreciable difference to develop. Geographic isolation of a type may also limit the applicability of the character.

INFERIOR CHEEK-TEETH

The variation displayed by the characters of the lower cheek-teeth is similar to that seen in the superior dentition. The inferior dentition presents no character whose value is comparable to that of the protocone or of the curvature of the crown of an upper cheek-tooth. Age assignments on the basis of characters exhibited by lower cheek-teeth are less satisfactory than for upper teeth. The relationships of forms based on lower cheek-teeth frequently depends upon an association of these teeth with the upper dentition. Only the more frequently used characters will be discussed. As in the case of the superior dentition, observations have been limited to teeth whose crowns have been less than one-third removed by wear.

Metaconid-metastylid column—In the collection of teeth from the Merychippus Zone this column varies in anteroposterior diameter from over one-half to less than one-fourth of the anteroposterior diameter of the crown. The groove or gutter on the inner wall may be sharply incised or open. The groove may be narrow or wide transversely and varies in size and shape with wear of the tooth. The characters of this column in P$\overline{2}$ are variable to a much larger extent.

In *Hipparion* the gutter between metaconid and metastylid is, as a rule, broadly open and displays a greater tendency to widen toward the base of the crown than in other genera. In advanced forms of *Hipparion* this column sometimes occupies most of the internal side of the tooth. The distinction between similar species of *Hipparion* and *Merychippus* on the basis of this column is frequently made with difficulty, since in many teeth of *Merychippus,* whose characters approach those of *Hipparion,* the metaconid-metastylid column is often similar to that found in the more progressive genus. In specimens whose structural features are transitional from those of *Merychippus* to those of *Protohippus* and *Pliohippus,* this character is of little help in affording a generic determination. It is of interest to note that Gidley [1] concluded from an examination of a large number of teeth of *Equus* and of the Loup Fork genera of horses that the type of metaconid-metastylid column in these forms presented great variability and possessed extreme unreliability in specific determination.

Posterior Lobe of M$\overline{3}$—In all the collections studied, the development of the posterior lobe of the third molar has been found variable to a degree which renders this character unreliable for purposes of generic and specific determination.

Entoconid—The shape of the entoconid has been used by Merriam [2] in distinguishing *Merychippus, Pliohippus,* and *Hipparion.* Merriam states: "In general the entoconid of *Merychippus* and *Pliohippus* species is truncated obliquely on the anterointernal angle by a plane or curved face, extending outward and forward from the inner side, while in *Hipparion* this region is expanded and the cross-section of the entoconid tends to take on a rectangular outline, instead of the approximately triangular section seen in *Merychippus,* or the triangular to imperfectly rectangular but anteroposteriorly short section seen in *Pliohippus.*" In teeth from the Merychippus Zone, this cusp varies in outline from triangular to completely rectangular. A study of teeth referred to the above three genera indicates that this cusp has no value in specific determination and that it must be employed with care in distinguishing genera. Merriam's use of this character applies to distinctions between advanced forms of *Hipparion* and *Pliohippus* on the one hand and the primitive and intermediate stages of *Merychippus* on the other.

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[1] J. W. Gidley, *op. cit.,* 105, 1901.

[2] J. C. Merriam, Univ. Calif. Publ. Bull. Dept. Geol., vol. 10, 131-132, 1916.

Entostylid—The posterior extension of the entostylid in molar teeth is variable. In general, it is greatest in unworn teeth and decreases with wear. This cusp is larger in molars than in premolars, but presents no peculiarities of taxonomic value.

Protoconid and Hypoconid—The external walls of these cusps are curved to varying degrees in the material from north Coalinga. In *Equus* the outer walls of the protoconid and hypoconid are flattened in contradistinction to the curved or convex walls of *Pliohippus.* An examination of teeth from localities assigned to the upper Pliocene and lower Pleistocene has convinced the writer that this character must be used with care in distinguishing *Plesippus* from either *Pliohippus* or *Equus.*

Cement—An examination of hundreds of specimens indicates that the amount of cement present on a lower tooth has no diagnostic value.

Supplementary Folds—The antero-external fold may be present or absent in the material from the Merychippus Zone. When present, the strength of this style varies considerably with the individual as well as with the extent of wear of the tooth. An antero-external fold of the enamel wall is frequently present in lower teeth of *Hipparion.* Its occurrence seems to be rather rare in *Pliohippus.* However, it has been observed in a series of lower teeth referred to *Plesippus shoshonensis* Gidley from the Idaho Pliocene. Presence of a fold or one or more plications of the enamel walls of the valley between protoconid and hypoconid has been observed in *Merychippus, Hipparion, Plesippus* and *Equus.* Its presence in so many genera would seem to invalidate its use as a specific character.

Occlusal Surface—The shape of the occlusal surface varies in a manner similar to that of upper cheek-teeth. Anteroposterior-transverse ratios obtained in the first and second molars at approximately the same stage of wear of the crowns vary from 1.70 to 2.10. In greatly worn teeth this ratio may have a value approximating 1.00. The extremes of this ratio are sufficiently removed to include most of the Equidæ.

Enamel Pattern—As in superior cheek-teeth, the complexity of the enamel pattern is well marked in *Hipparion* and in advanced forms of *Merychippus,* approaching the former genus. The extent of plication of the enamel walls of the lower cheek-teeth possesses a value for determination similar to that seen in the superior dentition.

Height of Crown—As in the superior dentition, this character is probably of great value in the distinction of species. The statements made for the superior dentition apply equally as well to the lower cheek-teeth. A table based upon measurements of lower teeth gives the following values in centimeters:

Horizon	Species	Maximum	Mean	Minimum
Mascall	*M. isonesus*	3.9	3.0	2.7
Coalinga	*M. californicus*	4.4	3.4	2.6
Barstow	*M. sumani* and *M. intermontanus*	4.4	3.5	2.8
Tonopah	*Merychippus*, sp.	4.8	3.6	3.1

VIEWS OF OTHER AUTHORS

The variation in tooth characters as observed by the writer is not unusual. Thus, Simpson,[1] in a study of the Miocene Vertebrate Faunas of Florida, found the characters of *Parahippus* grading into those of *Merychippus*. Gidley,[2] in a study of the genus *Equus* and of the Loup Fork genera, after determining the presence of considerable variation in characters of the cheek-teeth, concluded that many of the species of *Equus* ought not to be regarded as valid forms. To quote from Gidley:

> "An application of the foregoing principles of the variability of tooth characters to the specific definitions of Owen, Leidy and Cope shows the unreliability of most of the characters they have employed. Thus, the degree of complexity of the enamel folding is seen to be greatly affected by both age and individual variability—a fact which must be correctly understood before this character can be of even subordinate value as a specific determinant; the other characters given by these authors have been shown to be so affected by age or individual variability, or both, that no dependence can be placed upon them; . . ."

A wide range of variation was found by Matthew[3] in the *Merychippus* material from the Sheep Creek and Lower Snake Creek horizons in western Nebraska. Matthew met this difficulty by assigning over ninety per cent of the material to one species:

> "Within the material that I have referred to *M. paniensis* there is a wide range of variation, in size, length of crown and other proportional characters,

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[1] G. G. Simpson, Florida State Geol. Surv., Bull. 10, 21-27, 1932.

[2] J. W. Gidley, *op. cit.*, 105, 1901.

[3] W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 50, 159, 1924.

in the degree of union of the protocone, the development of the hypostyle, thickness of external styles, complication of the enamel on the lake borders, etc."

In commenting on the inadvisability of making a large number of species from the material he remarks:

> "The thousands of isolated teeth or other fragmentary specimens would clearly show that there are no constant or uniformly associated distinctions between such 'species'."

Again, Matthew and Stirton[1] in their description of the Pliocene Equidæ from Texas state in regard to the variation of tooth characters in *Pliohippus* that:

> "There is considerable variation in the size of the teeth, and some variation in height and curvature of the crown of the upper molars, in form and size of protocone, heaviness of mesostyle, tendency to union between protocone and hypocone, width of cement lakes and the development of the enamel inflections along their borders, and in probably all tooth-characters that have been used by all authors to distinguish species in the genus."

Merriam[2] in discussing the relationships of *Hipparion mohavense* from the Ricardo beds of the Mojave Desert, California, points out that:

> "With the collections now available, few if any diagnostic characters in form or pattern of the Ricardo teeth designated as *H. mohavense* appear which may be considered as certainly separating them from the Chinese *H. richthofeni.*"

Then, with regard to the relationships of *Hipparion richthofeni* to the European species, *H. gracile,* Merriam[3] states that:

> ". . . some of the characters which have been used to separate *H. richthofeni* from *H. gracile* seem to disappear with the study of large collections."

Again, Merriam[4] in his report on the horses of Rancho La Brea states that the variation within this group is sufficient to include some of the teeth of several Pleistocene species and of *Equus caballus.* With regard to the value of tooth characters he states:

> "While it is doubtless true that good specific differences appear in the enamel pattern of the cheek-teeth, it is certain that such characters must be used with caution. The final determination of the value of these characters must depend upon examination of considerable series of individuals of nearly the same age."

In his description of the merychippine forms from the Barstow of the Mojave Desert, Merriam described three species with the expectation that additional material would present characters more clearly demarcating the species.

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[1] W. D. Matthew and R. A. Stirton, Univ. Cal. Publ., Bull. Dept. Geol., vol. 19, 358-359, 1930.

[2] J. C. Merriam, Univ. Calif. Publ., Bull. Dept. Geol., vol. 11, 557, 1919.

[3] J. C. Merriam, *ibid.*

[4] J. C. Merriam, Univ. Calif. Publ., Bull. Dept. Geol., vol. 7, 413, 1913.

A somewhat different result was reached by Sefve[1] in his description of the Hipparions from North China. On account of the wide variation exhibited, he describes as few species as possible and expresses the opinion that additional material will serve to divide his original groups into a larger number of more clearly demarcated species.

> "Man muss auch hierbei darauf Rücksicht nehmen, dass die Variation in Wirklichkeit beträchtlich grosser gewesen ist als die Zahl der Arten erscheinen lässt. Wie aus meinen Artbeschreibungen hoffentlich hervorgeht, ist die Variation auch innerhalf der Arten sehr gross. Ich habe absichtlich so wenig Arten als möglich aufgestellt. Neue und vollständigere Funde werden warscheinlich zeigen, dass viele von den jetzt vorhandenen Variation, die ich bis auf weiteres nur als solche innerhalf der Art rechne, in Wirklichkeit verschiedene Arten repräsentieren."

In the opinion of the writer, the addition of more material from the Barstow and Chinese horizons will serve mainly to fill the ranks of teeth, whose characters are intermediate, rather than to aid in more sharply defining the established species.

CONCLUSIONS

The variation of tooth-characters as exhibited by the hundreds of specimens studied by the writer from horizons distributed throughout the later half of the Tertiary and by studies of the descriptions of many authors, indicates that there are no hard and fast distinctions to be made between the various species and genera of the Equidæ. With the collections at hand at the California Institute, gradational series with almost no discernible break can be built up from *Parahippus* through intervening genera to *Equus* and *Hipparion.* The selection, from horizons closely related in time, to form these series does not need to conform necessarily to the exact stratigraphic sequence of the deposits determined by the entire fauna from each locality. The characters which distinguish a species or genus unquestionably grade into the diagnostic peculiarities of other succeeding and preceding species and genera. The vertical stratigraphic range of the characters peculiar to a single form seems usually to be greater than that of a single stratigraphic horizon as determined by the entire fauna. Every large collection studied from a single horizon contains, in addition to teeth unquestionably referable to the species peculiar to that horizon, specimens whose characters can be regarded as intermediate and in addition specimens whose characters would allow them to be referred to other species from either slightly higher or lower horizons. Due to the overlapping of characters of various species, individual teeth are found with characters which would permit their assignment with equal right to any one of several species. When such a tooth is found, its stratigraphic value is defined by the total time range of the several species to which it might be assigned. In most cases this vertical range is considerably greater than the divisions of geologic time distinguished on the basis of a large and varied vertebrate fauna.

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[1] I. Sefve, Paleontologica Sinica, Series C, vol. 4, fascicle 2, 84, 1927.

Refinements in application of the characters of cheek-teeth of fossil horses to stratigraphy do not lie in a radical revision of our present conception of a species. If the gradation of characters be taken as indicating synonymy, the results ultimately become absurd. The enlargement of the boundaries of a single species or genus merely serves to enlarge the stratigraphic range of that species or genus. From a purely taxonomic point of view, the inclusion of a large number of variants within a single species defeats the object of the description of these forms. The placing of a large number of variants within a single species fails not only to convey a satisfactory impression of the appearance of a collection, but also results in the establishment of an unwieldy group of taxonomic units for future workers to handle. The setting up of three species by Merriam in the case of the Barstow material has a value for future workers which is considerably greater than that which would arise if all of the forms were included under one species. Although characters intergrade and although the variation of any one character is for the most part independent of the variation of any other character, the illustration of several types representing several distinguishable averages is of considerable value. On the other hand, the division of a group into a number of poorly defined species increases the complexity of the problem.

The dividing lines between genera and species are not drawn at natural breaks, but frequently serve to emphasize the gaps in our knowledge of an evolutionary line. As more and more material becomes available, the boundary lines between individual groups become less and less distinct. While species within any one horizon may usually be clearly demarcated on the basis of frequency curves, the addition of material from horizons only slightly removed in time tends to run together the boundaries of such frequency curves. In such instances the maxima become closely crowded and are of little value. It should be recognized that the characters of some specimens will necessarily have to remain intermediate in nature and that they should be so defined.

For purposes of stratigraphy, the association of structural types comparable to various type specimens permits of greater accuracy in age determinations of sedimentary deposits. An examination of many collections discloses the fact that during a part of the interval of geologic time in which the characters distinguishing a type specimen existed, these characters are associated with the gradually disappearing characters of a more primitive type, and that during another part of this time the characters of a more advanced type are appearing. The time required for one species to appear, reach its maximum development and disappear may be divided on the basis of the association of the central type with other advanced and primitive forms.

For the upper half of the Miocene of the Pacific Coast and Great Basin Provinces, the following associations appear to be of value and are in accord with the age determinations based on the evidence furnished by the entire fauna from each locality:

1. MASCALL—Associated with *Merychippus isonesus* are teeth referable to *M. relictus* and *M. seversus, Parahippus brevidens* and *P. avus.* Some of the more progressive teeth referred to *M. isonesus* are similar in aspect to teeth from the Merychippus Zone. *M. relictus* and *M. serversus* are small primitive types not found in the north Coalinga horizon. They would probably be found in horizons slightly earlier than the Mascall. The small species indicate an upward limit to which the Mascall might be assigned, while *M. isonesus* and "*M. californicus*-like" teeth suggest a lower limit. In addition, the merychippine milk-teeth from this horizon exhibit primitive conical cusps in contradistinction to the cylindrical shapes found in higher zones. The two species of *Parahippus* furnish further suggestions as to relative age of the assemblage. *P. avus,* though large, is a primitive form and has not been found in horizons higher than the Mascall. *P. brevidens* makes its first appearance in the Mascall and continues on into the time represented by the Merychippus Zone. The Skull Spring and Virgin Valley faunas occupy positions more nearly correlative with the Mascall.

2. MERYCHIPPUS ZONE—This horizon is characterized by the association of *Merychippus californicus* with teeth similar to the types of both *M. isonesus* and *M. sumani* and *Parahippus brevidens. M. isonesus* and *P. brevidens* reflect the time relationship which exists between the Merychippus Zone and Mascall. *M. sumani* indicates that the Barstow stage is not far removed.

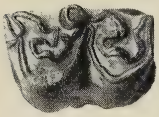
3. BARSTOW—Teeth similar to the referred specimen of *Merychippus californicus,* No. 1405 Calif. Inst. Tech. Coll., from the Merychippus Zone, are present in the Barstow formation of the Mojave Desert and these now represent the most primitive type. *M. sumani* is abundant and is associated with *M. intermontanus,* a horse of which some of the tooth characters are similar to *Protohippus. M. intermontanus* furnishes an indication that the Barstow should be regarded as higher than the Merychippus Zone.

PLATE 1

Merychippus brevidontus n. sp.

FIGS. 1 to 8—Figs. 1 to 1c, referred specimen, $\mathrm{P}\overline{4}$, No. 1431; figs. 2 to 2c, referred specimen, $\mathrm{M}\overline{1}$, No. 1427; figs. 3 to 3b, type specimen, *$P\underline{3}$, No. 1414;* figs. 4 to 4b, referred specimen, unworn $\mathrm{M}\underline{1}$, No. 1409; figs. 5 to 5b, referred specimen, $\mathrm{P}\underline{4}$, No. 1410; fig. 6, paratype, $\mathrm{M}\underline{1}$, No. 1422; fig. 7, paratype, $\mathrm{P}\underline{4}$, No. 1413; fig. 8, paratype, $\mathrm{M}\underline{2}$, No. 1408; x 1.

Calif. Inst. Tech. Coll. Merychippus Zone, California.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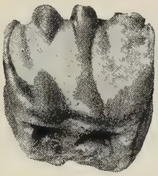
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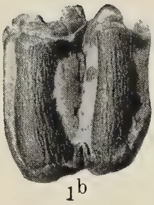
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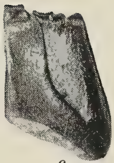
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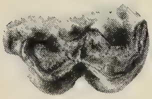
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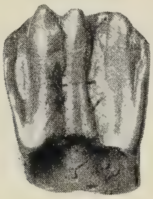
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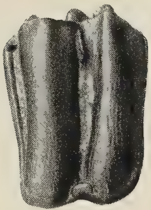
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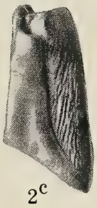
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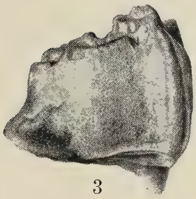
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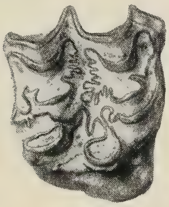
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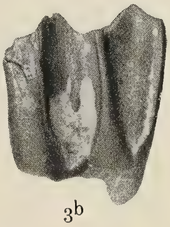
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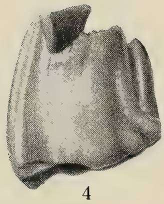
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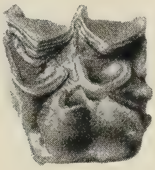
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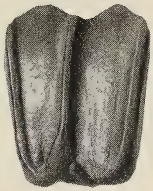
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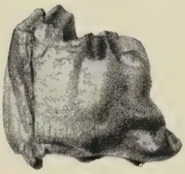
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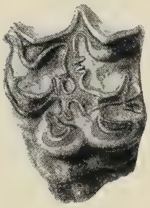
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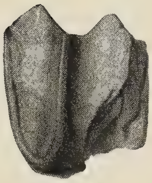
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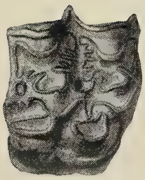
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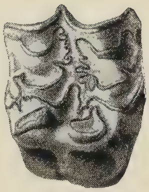
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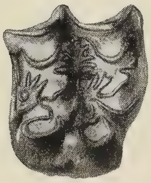
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PLATE 2

Merychippus intermontanus Merriam

FIG. 1—Superior milk-tooth series (protocone region of Dp$\underline{3}$ restored by illustrator), No. 21640; x 1.

Univ. Calif. Coll. Barstow Upper Miocene, California.

Merychippus californicus Merriam

FIG. 2—Superior milk-tooth series, No. 1500; x 1.

Calif. Inst. Tech. Coll. Merychippus Zone, California.

Merychippus isonesus (Cope)

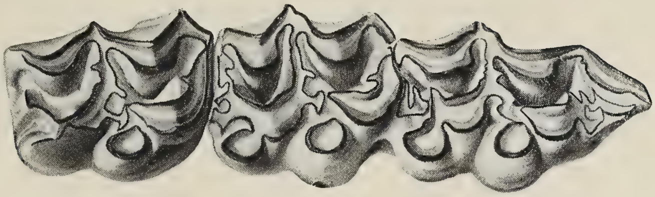
FIG. 3—Superior milk-tooth series, No. 544; x 1.

Calif. Inst. Tech. Coll., Locality 124. Skull Spring Middle Miocene, Oregon.

Merychippus brevidontus n. sp.

FIGS. 4 to 12—Referred specimens. Fig. 4, P$\underline{4}$, No. 1418; fig. 5, M$\underline{3}$, No. 1423; fig. 6, M$\underline{2}$, No. 1420; fig. 7, M$\underline{1}$, No. 1419; fig. 8, P$\underline{4}$, No. 1415; fig. 9, P$\underline{3}$, No. 1411; fig. 10, M$\underline{2}$, No. 1430; fig. 11, M$\overline{1}$, No. 1426; fig. 12, P$\overline{4}$, No. 1429; x 1.

Calif. Inst. Tech. Coll. Merychippus Zone, California.



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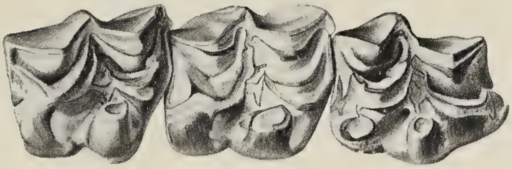

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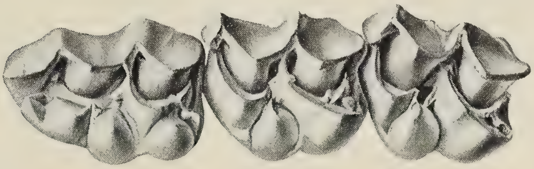

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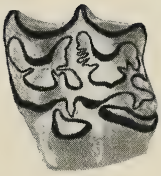

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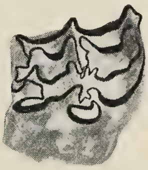

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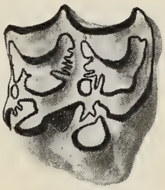

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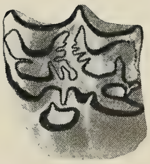

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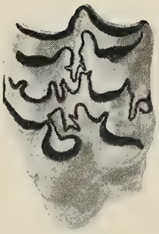

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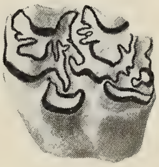

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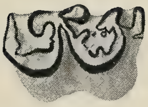

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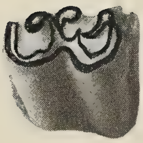

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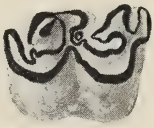

12

CONTRIBUTIONS TO PALÆONTOLOGY

VI

THE FAUNA OF THE MERYCHIPPUS ZONE, NORTH COALINGA DISTRICT, CALIFORNIA

By Francis D. Bode

With two plates and ten text-figures

[Issued July 20, 1935]

CONTENTS

Page

Introduction.......... 67

Location and Occurrence.......... 67

Fauna of the Merychippus Zone.......... 70

Frequency of Occurrence of Individuals.......... 71

Mode of Accumulation.......... 72

Environment of Fauna.......... 77

Stage of Evolution and Relationships of Fauna.......... 79

Stratigraphic Position in Marine Tertiary Series.......... 80

Age of the Merychippus Zone.......... 84

Systematic Description of Fauna.......... 86

- Carnivora.......... 86
  - Tomarctus sp.......... 86
  - Ælurodon sp.......... 87
  - Amphicyon sp.......... 88
  - Hemicyon(?) sp.......... 88
- Rodentia.......... 89
  - Monosaulax sp.......... 89
- Proboscidea.......... 89
  - Miomastodon or Trilophodon(?) sp.......... 89
- Perissodactyla.......... 90
  - Hypohippus sp.......... 90
  - Archæohippus mourningi (Merriam).......... 91
  - Parahippus brevidens Marsh.......... 91
  - Merychippus brevidontus Bode.......... 92
  - Merychippus californicus Merriam.......... 92
  - Rhinocerotid cf. Aphelops.......... 93
- Artiodactyla.......... 93
  - Prosthennops(?) sp.......... 93
  - Camelidæ.......... 93
  - Blastomeryx (Dyseomeryx) sp.......... 95

THE FAUNA OF THE MERYCHIPPUS ZONE, NORTH COALINGA DISTRICT, CALIFORNIA

INTRODUCTION

The fauna from the Merychippus zone, north of Coalinga, California, was first described by J. C. Merriam[1] in 1915. The assemblage as listed by Merriam included four genera of land mammals, namely, *Merychippus, Prosthennops, Procamelus* and *Tetrabelodon.* As recognized by Dr. Merriam, the discovery of mammalian remains in the marginal marine series of California possesses particular significance in that it furnishes an important aid in determining the time relationships between the marginal marine deposits of the Pacific Coast and the continental formations of the Great Basin and Great Plains areas of North America. The present studies were initiated, therefore, with a view to enlarging the fauna from this horizon and to establishing more accurately the time relationships of the assemblage. Moreover, it seemed desirable to record information concerning the mode of accumulation of the fossiliferous deposits and of the ecologic conditions under which the fauna existed.

Field work was conducted by the California Institute of Technology from 1928 to 1932, with the exception of the summer seasons. Much of the fossil material on which the present report is based was obtained by the late E. R. Inglee, field assistant in palæontology at the California Institute. A study of the assemblage from the Merychippus zone was suggested by Dr. Chester Stock, to whom the writer is indebted for helpful criticism in the course of the investigation. Dr. R. D. Reed, Chief Geologist for the Texas Company in California, furnished valuable information regarding the stratigraphic position of the Merychippus zone in the marine Tertiary section exposed near Coalinga and correlated horizons in oil well sections of the north dome of the Kettleman Hills. The plates and illustrations of fossil specimens were prepared by Mr. John L. Ridgway.

LOCATION AND OCCURRENCE

The horizon from which the fossil material was obtained is located on Domengine Creek (see Plate 1, fig. 1), on the east flank of the Diablo Range, 12 miles north of Coalinga, Fresno County, California. The north dome of the Kettleman Hills lies approximately 25 miles to the southeast. The general course of Domengine Creek is perpendicular to the strike of the sediments, but at a point approximately 4 miles from its mouth, the stream turns and flows south along the strike for nearly one quarter mile, thence resuming its easterly direction. The fossiliferous beds comprising the Merychippus zone outcrop along this north-south course and the type locality occurs on the east bank of Domengine Creek at an elevation approximately fifty feet above its bed. The accompanying chart (fig. 1) shows the geographic location of Domengine Creek on the west side of the San Joaquin Valley and its position with reference to the Diablo and Temblor Ranges and to the several oil fields occurring between Coalinga and McKittrick. It is by means of correlations with the subsurface sections from these oil fields and the surface sections in the Diablo and Temblor Ranges that the stratigraphic position of the Merychippus zone is determined.

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[1] J. C. Merriam, Trans. Amer. Philos. Soc., n.s., vol. 22, art. III, 1915.

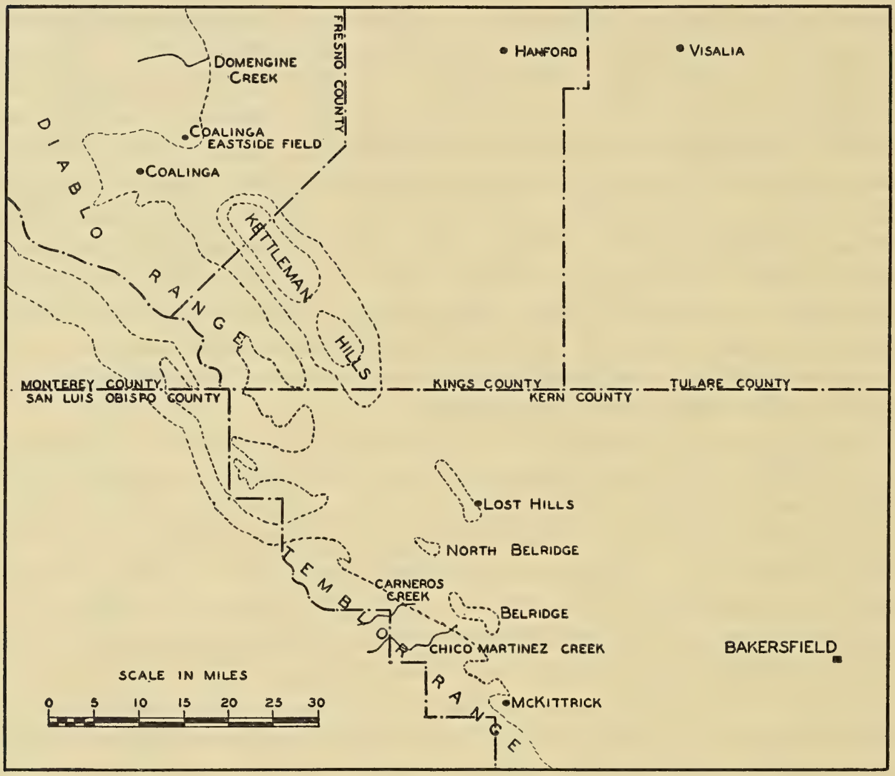

FIG. 1—Map of portion of west side of San Joaquin Valley showing geographic position of Domengine Creek in relation to Coalinga and to various oil fields and surface areas with which stratigraphic correlations are made.

The original material described by Merriam from the Merychippus zone was obtained from sandstones and conglomerates, 2 to 3 feet in thickness, lying at the top of the so-called Miocene "Temblor" section on Domengine Creek and immediately below Miocene beds known locally as the "Big Blue." This field locality has been recorded in the catalogues of the California Institute of Technology as No. 108. The major portion of the material obtained by the Institute was collected from pockets at this same stratigraphic level. In addition, however, a considerable quantity of material was collected at a point farther south along the strike of the beds and approximately twenty feet stratigraphically below the level of locality 108 (see Plate 1, fig. 2). This locality is known as No. 129. No differences have been noted between the two assemblages. The position of locality 129 in the series gives added reason for regarding the Merychippus fauna as occurring within the "Temblor" as indicated by Merriam, and not in the base of the Big Blue.

The underlying one hundred feet of sediments increase gradually in coarseness as they approach the Big Blue contact, the deposits changing gradually from alternating shales and fine sandstones to sandstones, and then to coarse sandstones and pebble conglomerate lenses. Throughout the upper twenty feet cross-bedding is visible in the sandstone. The three feet of sediments underlying the Big Blue consist for the most part of sandstones containing lenticular pebble conglomerates. Here lenses are numerous and give the false appearance of a continuous bed. Closer examination reveals, however, that none of them extends along strike for more than twenty feet. Their continuous appearance is due largely to their abundance. Excavations show that the average width of these lenses, down the dip, is usually equal to half their length along the strike, giving them a lateral ellipsoidal area with an elongation approximately in the direction of strike. Frequently small pockets of clay are found within and underlying the conglomerates. Clay pockets not associated with pebble lenses have also been observed. While fossil mammalian remains are found scattered throughout a hundred feet stratigraphically, the material becomes abundant only in the upper twenty feet. At this level the material is usually concentrated in the conglomerates and is most abundant at the top of the section. Here the number of horse teeth frequently exceeds that of the larger pebbles. Small concentrations of specimens have also been found in clay pockets not associated with the conglomerates. Fossil material has been found northward from the lower bend on Domengine Creek to a point where the fossiliferous strata disappear under the grassy mantle of the top of a ridge, a distance of nearly a thousand feet. Only scattered remains were found along the strike of the beds, on the south and west side of Domengine Creek. In this direction the conglomerate lenses disappear, leaving the Big Blue in contact with sandstones. The zone of maximum concentration has a lateral extent along the strike of approximately four hundred feet. Its extent in the direction of the dip of the beds is unknown.

With the exception of three horse rami, the material from the Merychippus zone consists entirely of scattered teeth and fragments of limb elements. But few of the teeth show signs of abrasion, although many of the specimens exhibit a tendency to shatter into many fragments when removed from the matrix. The skeletal material, on the other hand, is usually so well rounded that few characters of taxonomic value are available. The relatively compact carpal and tarsal bones are the most numerous skeletal parts represented. In this collection the astragali far outnumber other elements. As with the teeth, the skeletal material is assignable principally to the Equidæ. Upper limb material is rare and is represented by one complete horse metapodial and a score or more of fragments of the articulatory portions. Among upper limb specimens, camel and horse are equally well represented, offering a point of contrast with remaining parts of the skeleton which belong chiefly to members of the Equidæ. Presence of rhinoceroses and of mastodonts is indicated by remains of cheek-teeth. No large limb material referable to these forms has been found. Bone material of large size is completely absent in the deposits, the larger fragments never exceeding a maximum diameter of four inches. Sharks teeth are plentiful and are associated with an occasional tooth fragment of the aquatic mammal *Desmostylus* in all the quarries. No skeletal parts of these forms have been found. Mud casts of a gastropod and of a lamellibranch were found in one of the fossiliferous pockets at locality 129.

FAUNA OF THE MERYCHIPPUS ZONE

The following species are now recognized in the collections from the Merychippus zone:

Carnivora:
    Tomarctus sp.
    Ælurodon sp.
    Amphicyon sp.
    Hemicyon? sp.

Rodentia:
    Monosaulax sp.

Proboscidea:
    Miomastodon or Trilophodon? sp.

Perissodactyla:
    Hypohippus sp.
    Parahippus brevidens Marsh
    Archæohippus mourningi (Merriam)
    Merychippus brevidontus Bode
    Merychippus californicus Merriam
    Rhinocerotid cf. Aphelops

Artiodactyla:
    Prosthennops sp.
    Procamelus sp.
    Oxydactylus? or Alticamelus? sp.
    Miolabis? sp.
    Blastomeryx (Dyseomeryx) sp.

Marine vertebrates as follows:
- Cetacean remains
- Desmostylus cf. hesperus Marsh
- Selachian teeth
  - Carcharodon
  - Lamna
  - Isurus
  - Odontaspis?
  - Teleosts

FREQUENCY OF OCCURRENCE OF INDIVIDUALS

Individuals assigned to the species *Merychippus californicus* far outnumber all other forms in the fauna from the Merychippus zone, this species being represented in the collections by more than two thousand well-preserved cheek-teeth. At least five hundred additional teeth were discarded because of their fragmentary preservation, when the collections from the field were prepared in the laboratory. Moreover, many specimens, too incomplete to collect, were discarded in the field. According to E. R. Inglee the numerical relation of complete and incomplete teeth encountered to those actually shipped was well over five to one. It appears safe to assume that more than five thousand teeth were encountered during the progress of the excavations. On the basis of the scattered distribution of the teeth removed from the Merychippus zone, it seems likewise safe to assume that not all of the twenty-four cheek-teeth assignable to one individual are included in the collections. A reasonable estimate of the minimum number of individuals obtained may be placed at two hundred and fifty. The number of individuals indicated by third upper molars of the right side is one hundred and twenty. However, because of the teeth discarded and the probability that not all individuals in the collections are represented by the third molar, the former estimate is regarded as being nearer the actual number.

The number of individuals of species other than *Merychippus californicus* has been determined from the total number of teeth in the collections after taking into account the size, shape and stage of wear of all teeth occupying opposite but similar positions in the skull or mandible. The possibility of duplication of number arising from counts of lower and upper teeth actually representing the same individual has been taken into consideration.

With the exception of *Merychippus californicus* all other species in the collection are represented by less than one hundred teeth. The volume of rock excavated to obtain the present collection was well over a thousand cubic yards. Since the teeth were distributed rather uniformly through this volume and over an area of at least six thousand square feet, it seems likely that not many of the specimens belong to the same individual. In the case of all species the number of individuals is probably a minimum. However, since the same procedure has been followed for all forms and since the number of merychippine teeth greatly exceeds that of all other forms, the relative frequency of occurrence of all forms is considered to be essentially correct.

The accompanying chart (fig. 2) shows graphically the representation of individual groups, but for those mammals in which relatively few individuals per species are known, only the size of the family is shown.

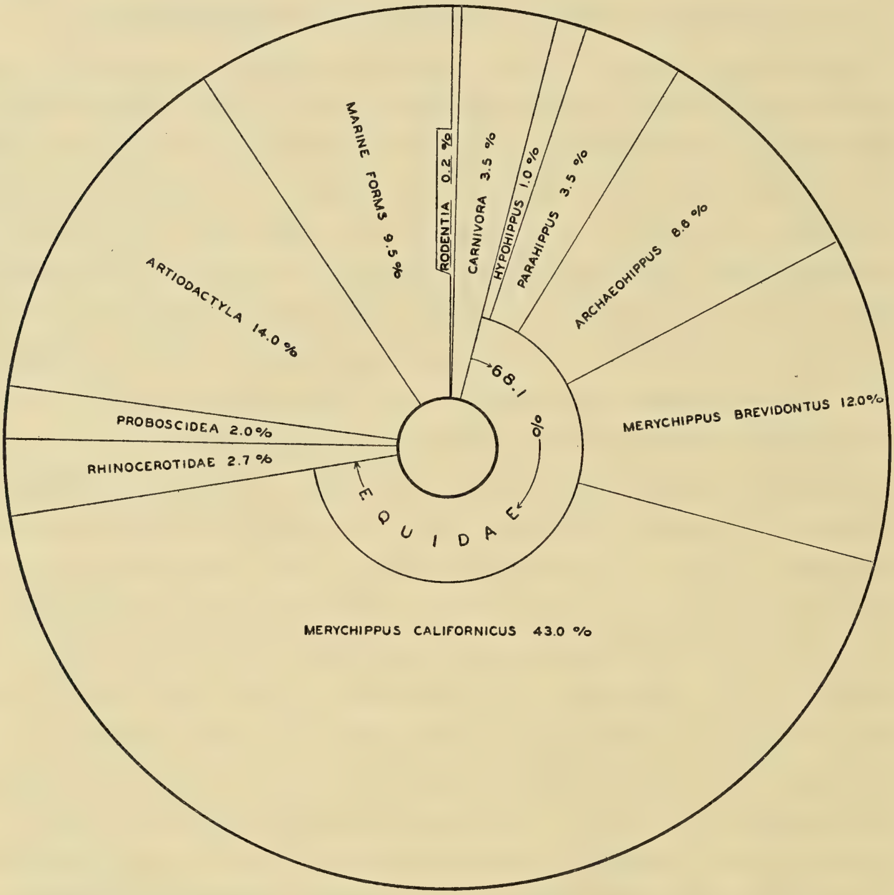

FIG. 2—Chart showing percentage of frequency of occurrence of individuals in fauna of Merychippus Zone.

MODE OF ACCUMULATION

The relative abundance of sharks teeth and the presence of *Desmostylus* and of several other marine forms indicate the marine origin of the deposits containing the Merychippus zone. The preponderance of remains of land mammals, on the other hand, suggests that the accumulation took place in an area close to shore, at a locality where fragments of these forms were readily obtainable. That the accumulation occupied a period of time of greater duration than a few years is suggested by the fact that the fossil material is found distributed throughout the upper hundred feet of the "Temblor beds" in the Domengine Creek section. The gradual increase in coarseness of the sediments, accompanied by a similar increase in concentration of fossil material toward the top of the section, may be interpreted as indicating the approach of a land area. The "Temblor" section on Domengine Creek has a thickness of four hundred and eighty feet. Six miles south, on the Coalinga anticline, this formation has a thickness of approximately six hundred feet.[1] In axial wells on the north dome of the Kettleman Hills the Temblor has increased in thickness to approximately fifteen hundred feet.[2] This southward increase in thickness suggests that the land area from which the material was derived lay to the north and possibly to the northwest. The northwest derivation of the material forming the Big Blue may be regarded as corroborative evidence.[3]

As previously mentioned, the fossil material occurs as scattered teeth and small fragments of limb elements buried in ellipsoidal conglomerate lenses. It would appear quite likely, from the nature of the occurrence, that the fossil material accumulated on a sandy surface of the sea floor over which were scattered more or less elliptical pebbly areas. Within the latter and especially at their bottoms occurred small concentrations of mud. These areas evidently lay in slight depressions on the floor. Apparently other small depressions contained only mud. Employing the terms defined by Twenhofel,[4] the pebble conglomerates are composed of a heterogeneous mixture of pebbles, granules, varying sizes of sands, and small quantities of mud. The sediments exposed on the surface surrounding the pebble areas were comprised mainly of medium to fine-grained sands. The maximum diameter of the pebbles rarely exceeds one inch, although particles closely approximating this size are numerous in the upper three feet of the "Temblor" sediments. In the pebbly areas and infrequently in the few clay pockets, fossil vertebrate specimens were found lodged between pebbles or were buried almost entirely in the clay. Invertebrate fossils are absent.

As indicated by the presence of marine vertebrates, the surface on which the accumulation took place lay submerged beneath salt-water. The maximum strength of the currents during the period of deposition is indicated by the size of the largest pebbles. These pebbles probably were rolled along the bottom, coming to rest ultimately in shallow depressions on the sandy floor. The clay or mud within the gravels may be regarded as material caught and protected from further movement after sinking through the interstices between the pebbles and coarse sands. Fossil material rolled along the bottom would also become lodged between the pebbles and thus resist further movement. The presence of fossils of slightly greater size than the pebbles may be accounted for by the lower density of this material.

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[1] G. C. Gester and John Galloway, Bull. Amer. Assoc. Petrol. Geol., vol. 17, 1180, 1933.

[2] G. C. Gester and John Galloway, *op. cit.*

[3] Robert Anderson and Robert W. Pack, U. S. Geol. Surv. Bull. 603, 83, 1915.

[4] W. H. Twenhofel and Collaborators, *Treatise on Sedimentation,* The Williams and Wilkins Co., 155 pages, 1926.

In reviewing the types of deposits under which the Merychippus zone may have accumulated, at least four possibilities present themselves. These may be indicated, with regard to the environmental conditions under which they are formed, as littoral, marginal lagoon, estuarine, and delta accumulations.

The stratigraphic position of the Merychippus zone at the top of the "Temblor," the type and distribution of the sediments, and the thickness of the deposit may be regarded as indications favoring a littoral origin of the deposits. However, several features are opposed to this type of origin of the Merychippus zone. While the absence of marine invertebrate fossils may have no significance, it seems more probable from the presence of other marine forms, that shell fragments would have been in evidence if the concentration north of Coalinga occurred under littoral conditions. The deposits laid down under a littoral environment are largely the result of wave action. Lack of abrasion of most of the fossil teeth from the Merychippus zone, some specimens preserving intact their long thin roots below the base of the crown, and the perfect preservation of the delicate structures of small teeth as in *Archæohippus* are some features of the organic remains which appear to mitigate against the postulate of accumulation on a wave-pounded beach. Moreover, it is difficult to conceive of large concentrations of fossil specimens (horse teeth sometimes outnumbering the pebbles), as forming on a beach.

A "marginal lagoon" is a body of water partially separated from the sea by a bar or barrier beach. Sediments from the land are brought in by fresh water and those from the sea by tidal currents. The water is usually salty. This type of environment might be regarded as favorable for the accumulation of sharks teeth and remains of land mammals. However, in a marginal lagoon the waters are quiet and as they periodically receive new sediments brought in by tides, the deposits become well stratified at the time of accumulation. The stratification of lagoonal deposits is even and regular and the sediments consist for the most part of fine mud and silts. Remains of invertebrates are usually abundant. These characteristics are not in accord with those exhibited by the deposits of the Merychippus zone.

Estuarine deposits are laid down in an enlargement of a river channel near its mouth, when the latter has been drowned through coastal subsidence. Tidal currents are commonly more active here than along the shores of the open sea, resulting in much scouring of the bottom. Remains of strictly marine invertebrates are uncommon. The sediments riverward are usually sands and silts, while those seaward are not unlike marine deposits. The intermediate estuarine area may have a bottom quite similar in appearance to that which probably prevailed in the locality of the Merychippus zone. With the exception of the absence of evidences of scoured channels, the deposits north of Coalinga present no other characteristics opposed to those seen in the bottom of estuaries. However, an estuary, primarily resulting from a subsidence of the coast, is in direct opposition to the probable conditions obtaining in the vicinity of the Merychippus zone during the time represented by the upper part of the "Temblor."

On the other hand, the deposits at the Merychippus zone present no characters serving to distinguish them from those of delta deposition. Delta deposits are divided into four classes;[1] the topset beds of the subaerial plain, the topset beds of the subaqueous slope, the deposits of the foreset slope, and the bottomset beds beyond the foreset slope. Sediments of the first two are characterized by sands and clays with gravel uncommon in the first. The bottomset deposits are similar to those deposited entirely under marine conditions.

Both river and marine waters are concerned with the deposition of sediments on the foreset slope, the former adjacent to the ends of river distributaries and the latter over the intervening areas. The coarsest materials of the delta are found here. These are usually deposited with an initial inclination, although the angles of inclination are usually low in large bodies of water. The upper portions of the foreset beds are deposited above wave base and the lower portions may be below that level. In turbid waters, marine organisms may be absent. The sediments of the foreset slope are poorly sorted but stratified, in contrast to evidence of scour channels seen in the subaqueous topset beds. The rather uniform stratification of the last hundred feet of the "Temblor" on Domengine Creek, the gradual increase in coarseness toward the top of the section, the uniformity of size of the pebbles and of their disposition along the strike, the presence of cross-bedding, the association of fossil types, the lenticular disposition of the conglomerates, are all in accord with this type of deposition. As judged in the light of the characters mentioned above, the Merychippus zone may be interpreted as an accumulation which took place in the subaqueous beds of a large river.

The subaqueous region of a delta deposit appears to account for all the characteristics of occurrence exhibited by the fossil material at the vertebrate localities north of Coalinga. The scene of deposition may be visualized as the region in front of the mouths of distributary streams and below the level of the sea, with a total area of accumulation whose width approximated one thousand feet, with a central area in which most of the material was concentrated within a width of approximately four hundred feet. The marine water above accounts for the presence of the shark teeth and other forms. The constant movement of sand and pebble particles along the bottom afforded the probable agent preventing population by marine invertebrates. The currents of the river over the subaerial part possessed a maximum strength capable of bringing pebbles up to one inch in diameter to the scene of accumulation. Within the areas of accumulation the water had sufficient strength to continue movement of the pebbles, but as these progressed seaward, less and less movement occurred. The specific areas of pebbles resulted from a trapping of this sedimentary material in shallow depressions from which the currents were unable to remove it. Clay, silt and slightly coarser particles, on sinking into the interstices between the pebbles, were thus protected from further movement. In like manner, isolated teeth and fragments of bones of land mammals were rolled seaward along the bottom. When a tooth or fragment became lodged between pebbles, it was able to successfully resist further movement. As the pebbly areas were built up, obstructions were developed which hindered for a time a seaward movement of the finer material behind them. Eventually, however, a stage was reached where the fine sediments washed over and buried the gravel areas, protecting them from further disturbance. A new depression to the side or behind probably originated by this action with consequent initiation of a new cycle of accumulation.

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[1] W. H. Twenhofel, *op. cit.*, 591–595.

The lower density of the teeth and especially of the bone material accounts for their larger size in comparison with that of the pebbles. As mentioned under occurrence, the teeth rarely show signs of rounding, many of the specimens still possessing all of their root portions. Transportation with rock material for a considerable distance would certainly be expected to remove all signs of the more fragile structures. This feature is suggestive of a relatively gentle process of transportation and seems to indicate that the river bringing down the material carried very little large material. This type of stream is generally characteristic of a country well covered by vegetation. The angularity and excellent preservation of the teeth indicate further that in all probability many of the teeth did not fall from the individual jaw or skull, to which they belonged, until these organic remains had reached a position close to the area of burial. The skeletal elements are nearly always rounded. This is to be expected, for after lengthy immersion bone is considerably softened, whereas teeth retain their hard structure for a much longer period of time. The rounding of the bone fragments is thus probably due as much to long immersion before burial as to abrasion during transportation.

None of the limb bones are complete, and large elements belonging to such forms as a mastodon or rhinoceros are entirely lacking. Skulls are also absent. These large skeletal parts were probably too heavy for transportation and were thus forced to lie upstream until disintegration developed fragments small enough to be transported.

The organic remains were probably acquired originally by the river as material washed from its sides and from tributaries. This appears to be a normal process, since animals frequently die near or immediately adjacent to stream courses. Unlike the case observed by Matthew[1] in his study of *Merychippus primus* from the Sheep Creek horizon of western Nebraska, the equine teeth from the Merychippus zone of California do not show ontogenetic stages of wear. Seasonal floods are thus insufficient to account for the acquisition of the material; rather does the acquisition appear to have been a continuous process. The type of deposit and its thickness suggest that the material required a period considerably longer than a brief span of years to be concentrated.

ENVIRONMENT OF FAUNA

While the merychippine horses were unquestionably the most prevalent mammals in the fauna of the Merychippus zone, their presence does not necessarily point to the existence of a wide-spread plain or steppe environment. These forms, in contrast to their living descendants, possessed quite clearly a number of more primitive structural characteristics in skull, skeleton and dentition, in which respect they were less favorably adapted to open country and to a diet comprised chiefly of gritty grasses. As a matter of fact, the hyposodont horses of to-day exist not only on the desolate plains of central Asia but are found also in open wooded country of South Africa and in the Himalayas. Thus a wooded region with interspersed grass-covered areas may be postulated as an environment particularly advantageous to the development of large numbers of merychippine horses.

In this connection it is significant to recognize likewise the presence and diversity of the brachydont horses in the fauna. Among the latter, *Hypohippus*, with its broad feet and brachydont teeth, seems well adapted to life in a wooded environment. *Parahippus*, with teeth similar to those of *Hypohippus*, was probably also a browsing type. *Archæohippus* may well have occupied an environment similar to that of the present day deer, forms more typical of wooded areas than of a plains environment. On the other hand, *Archæohippus* with its slender limbs can hardly be regarded as having a range restricted to small tree-covered areas along stream courses. Similar suggestions are offered by members of the camelidæ and by *Dyseomeryx*. These are all brachydont forms, whose habits are presumably akin to modern types occupying large wooded areas.

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[1] W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 50, 162–166, 1924.

The presence of rhinoceroses is not necessarily indicative of swampy ground since two of the living Indian species and both of the African forms are found in wooded areas adjacent to grassy plains. The living types feed on grasses and on the leaves of small shrubs and young trees. Judged in the light of its long limbs and brachydont teeth, *Aphelops* may have occupied a habitat featured by an open forest and its floral association including an undergrowth of grass.

The Proboscidea as represented in the fauna by the mastodonts were without much question browsing forms. Like the rhinoceroses, brachydont horses and camels, these forms were certainly not restricted to small tree-covered areas adjacent to stream courses.

The type of environment as here conceived readily admits of the presence of peccaries. The character of the carnivore assemblage suggests a plentiful food supply. Doubtless these forms found ample opportunity to stalk their prey.

Comparison of the fossil assemblage with a characteristic living assemblage of South Africa tends to emphasize the essentially normal numerical representation of individual types in the former. The large number of individuals of the Equidæ obtained from the Merychippus zone may be misleading from the standpoint of actual representation of these mammals in the contributing area. It is quite probable that these forms were abundant on the land areas, but it must be remembered also that the structure of an equine tooth is such as to withstand better the vicissitudes incident to burial than that of teeth of many other types. In addition, the protohippine horses may have been more susceptible than other forms to the processes which brought about their ultimate entombment in the record.

The fauna regarded as a unit suggests the presence of wooded country with sufficient ground-cover of grass to be attractive to both browsing and grazing types. An analysis of the fauna gives no special reason for recognition of a highly variable external environment. In view of the mobility of the types occurring in the fauna of the Merychippus zone, this assemblage doubtless furnishes a representative cross-section of the regional life of that time.

Additional information concerning the climate and vegetational cover of this region of California during Temblor time may be drawn from the fields of invertebrate palæontology and palæobotany. Thus Kleinpell[1] has pointed out that the foraminifera of the Temblor sea indicate warm and almost tropical conditions. Warm water during this period is indicated also by the megafossil fauna.

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[1] R. M. Kleinpell, paper on *A Proposed Biostratigraphical Classification of the California Miocene*, presented at a meeting of the Micropaleontological Society in Los Angeles, Nov. 1933.

According to Chaney[1] the fossil floras of western North America indicate rather uniform climatic conditions during the Miocene. Chaney considers the Mascall flora and its equivalents as related to the oak-madrone forests of California, where topographic conditions of low relief have no particular influence upon a vegetation resulting from a rainfall of approximately thirty inches.

STAGE OF EVOLUTION AND RELATIONSHIPS OF FAUNA

On the basis of present age-determinations of Tertiary vertebrate horizons in western North America, the Merychippus zone assemblage may be regarded as late middle Miocene in age. In its stage of evolution and in its relation to faunas of the Great Basin Province, the Merychippus zone occupies a position intermediate between the upper Miocene Barstow of the Mohave Desert and the middle Miocene Mascall of eastern Oregon. The Virgin Valley and Skull Spring faunas of northwestern Nevada and eastern Oregon, respectively, are currently regarded as approximately equivalent to the Mascall and their relationship to the fauna from the north Coalinga district is approximately comparable to that which the Mascall bears to the latter. The Merychippus zone fauna represents an intermingling of genera found either in the Barstow or in the Mascall. In general, the more progressive Mascall forms are found also in the horizon north of Coalinga. Likewise, types having affinities with Barstow species are usually found to be related to the more primitive forms in the fauna from the Mohave Desert. This relationship is particularly interesting in view of the fact that the Barstow fauna is distinctly advanced beyond that of the Mascall.

The Equidæ afford an excellent illustration of this intermediate position on the part of the fauna from the Merychippus zone. *Parahippus brevidens* is a species commonly occurring in the Mascall but not found in the Barstow. The Coalinga *Hypohippus* is considerably smaller than that found in the Barstow. However, the *Archæohippus* material from the Merychippus zone is clearly distinct from the Mascall species, *A. ultimus,* and is specifically inseparable from the Barstow form, *A. mourningi.* Within the Merychippus group the small species, *M. brevidontus,* is found also at Skull Spring and Virgin Valley. *M. brevidontus* represents a more primitive species than any of the Barstow forms. Among two thousand teeth representing the species *Merychippus californicus* a considerable number present characters which are indistinguishable from those of *M. isonesus* of the Mascall. An equal number of these teeth, on the other hand, possess characters identical with those of *M. sumani* from the Barstow. Thus the characters displayed by this species reflect the intermediate position of the fauna. The primitive Mascall species, *M. seversus* and *M. relictus*, are absent from the Coalinga fauna, as is also the progressive species *M. intermontanus* which is characteristic of the Barstow.

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[1] R. W. Chaney, Carnegie Inst. Wash. Pub. No. 349, 25, 1925.

Among the carnivores the *Amphicyon* material is close to *A. sinapius*, a species recognized in the Mascall fauna. *Amphicyon* has not been recorded from the Barstow. *Tomarctus* from the Merychippus zone is not clearly distinguishable from either the Mascall or Barstow types. The presence in the Coalinga fauna of a large dog referred to the genus *Ælurodon* and similar to *A. wheelerianus* from the Santa Fé, is another indication of Barstow affinities. *Ælurodon* is a more progressive form than related canids from middle Miocene horizons of the northwest. *Hemicyon* has not been recorded from the Mascall or Virgin Valley. However, a single upper carnassial from Skull Spring has been identified as belonging to this form. A lower molar from North Coalinga is comparable to the corresponding tooth of *Hemicyon barstowenses* from the Mohave Desert horizon.

The mastodont teeth, referred questionably to *Miomastodon* or *Trilophodon*, are similar in size to specimens from Virgin Valley. The proboscidean material from the Barstow is noticeably larger, although the difference in size may have no special significance.

Among the Artiodactyla, the camels offer some indication of the intermediate position of the Merychippus zone fauna. The largest of the Coalinga forms is comparable in size to the smallest members of the group referred to *Procamelus* from the Barstow.

Curiously, the genera *Dromomeryx* and *Merycodus*, although found in the Barstow assemblage and in the middle Miocene faunas of northwestern Nevada and eastern Oregon, are absent in the Merychippus zone. Possibly ecological conditions are responsible for this absence at the Coalinga locality.

A detailed comparison of the Merychippus zone fauna with the more important Miocene assemblages of the western Great Plains is unsatisfactory, due to incompleteness of information regarding a number of species occurring in the California horizon. On the basis of the stage of evolution of the Equidæ from the "Temblor" beds, this horizon represents an advance beyond the Sheep Creek or *Merychippus primus* zone of western Nebraska. The lower Snake Creek fauna differs from that of the Merychippus zone in the absence of *Ælurodon* and the presence of more progressive camels.

STRATIGRAPHIC POSITION IN MARINE TERTIARY SERIES

The type Temblor section described by F. M. Anderson[1] is located on Carneros Creek on the west side of the San Joaquin Valley northwest of the town of McKittrick. A similar section, also used for correlation purposes, is found on Chico-Martinez Creek a few miles farther south. At these localities, the top of the Temblor was placed by Anderson at the top of the so-called "Button Bed" sandstone. The Temblor is also somewhat loosely regarded as a stage name for beds containing the mollusk *Turritella ocoyana.* However, *T. ocoyana* has been reported from beds thought to be stratigraphically higher than the "Button Bed" on Carneros Creek,[1] and its value as a marker fossil for the Temblor is thus questionable.

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[1] F. M. Anderson, Proc. Calif. Acad. Sci., 3d ser., vol. 2, 156–247, 1905.

The next higher stage is the Monterey, deposits so called being regarded as equivalent to beds found in the type section on the Monterey Peninsula. At the base of the type section occurs the foraminiferal zone characterized by *Valvulineria californica,* one of the most wide-spread microfaunal zones known in the Coast Ranges of California.

At Chico-Martinez Creek and the type Temblor Section on Carneros Creek, the top of the Button Bed sandstone is separated from the base of the *Valvulineria californica* zone by two hundred and fifty feet of shales which Cunningham and Barbat called the Gould shale.[2] It is with reference to the Gould shale that that part of the Kettleman Hills' section, containing beds regarded as equivalent to the Merychippus zone, are correlated.

On Domengine Creek the beds assigned to the "Temblor" have a thickness of approximately five hundred feet. These beds lie unconformably above sandstones containing the "Leda zone" of the Kreyenhagen Group. The section is composed for the most part of alternating shales and sands increasing in coarseness toward the top of the section and containing the following recognizable units: (1) A thin zone of black or coaly clays sixty feet above the base. (2) A reef bed containing *Scutella merriami,* one hundred and sixty feet above the top of the coaly clay member. (3) White siliceous and diatomaceous shales fifteen feet in thickness, the "Indicator" bed of Arnold and Anderson,[3] forty-five feet above the top of the reef bed. The indicator bed may be traced southward across the Coalinga anticline. (4) The conglomerates containing the vertebrate fossils, one hundred and twenty feet above the indicator bed. (5) The overlying Big Blue is a large lens with a lateral extent of approximately twenty miles. This member is unusual in view of the fact that throughout most of its extent it consists of a compact mass of fine detritus made up of dust, flakes and pebbles of serpentine and, at some localities, conglomerates composed almost entirely of serpentine boulders. On Domengine Creek the Big Blue has a thickness of nearly two hundred and fifty feet. It is unconformably overlain by beds of upper Miocene, Santa

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[1] R. D. Reed, *Geology of California,* Pub. Amer. Assoc. Petrol. Geol., 219, 1933.

[2] C. F. Cunningham, and W. F. Barbat, Bull. Amer. Assoc. Petrol. Geol., vol. 16, 417–421, 1932.

[3] R. Arnold and Robert Anderson, Bull. U. S. Geol. Surv. 398, 81–82, 1910.

Margarita age. North of Domengine Creek, in the vicinity of Salt Creek, the Big Blue attains a maximum thickness of more than one thousand feet. In a southerly direction it varies in thickness from two hundred to forty feet and finally lenses out on the south flank of the Coalinga anticline, north of Coalinga.

In the vicinity of Oil Creek between Coalinga and Domengine Creek, Galloway[1] reports the presence of *Turritella ocoyana* in beds stratigraphically higher than the base of the Big Blue at the Merychippus zone locality. According to Reed,[2] north of Domengine Creek sandstones containing *T. ocoyana* are found overlying the Big Blue. Anderson and Pack[3] state that the fauna of the marine beds underlying the typical serpentinous shale occurs also in sandy beds interstratified with or overlying the Big Blue. The Big Blue and the underlying Merychippus zone are thus placed within the stratigraphic range of *Turritella ocoyana.*

The Domengine Creek section can be correlated with sections on the Coalinga anticline, which in turn are correlated with those penetrated by oil wells on the north dome of the Kettleman Hills.

Correlations of oil well sections from the north dome of the Kettleman Hills with the surface sections on Carneros and Chico-Martinez Creeks are made by means of successive comparisons southward of oil well sections from the south dome of the Kettleman Hills, the Lost Hills, North Belridge and Belridge oil fields.

The following chart (fig. 3) attempts to show this correlation. The data for the Domengine Creek section are based on observations by the writer, as well as from the section illustrated by Merriam[4] and from information furnished by Reed.[5] Information concerning the Coalinga anticline was derived from Reed's *Geology of California.*[6] Data for the Kettleman Hills were furnished by Dr. Reed and were obtained also from correlation charts illustrating the geology and stratigraphy of the area by Gester and Galloway, and by P. P. Goudkoff.[7] The Carneros-Chico Martinez Creek composite section was obtained from charts published by Goudkoff.[8] A correlation of the coaly clay member in the Domengine Creek section with the "lower variegated" in the Kettleman Hills and the base of the Big Blue with the base of the "upper variegated" was suggested by Dr. Reed.[9] The correlation of the base of the Big Blue with the "upper variegated" also follows

[1] John Galloway, Paper presented before Amer. Assoc. Petrol. Geol., Los Angeles, Nov. 1933

[2] R. D. Reed, personal communication.

[3] Robert Anderson and Robert W. Pack, *op. cit.*, 83, 1915.

[4] J. C. Merriam, *op. cit.*, 5, 1915.

[5] R. D. Reed, personal communication.

[6] R. D. Reed, *op. cit.*, 1933.

[7] G. C. Gester and John Galloway, *op. cit.*, 1169 and 1180, 1933; P. P. Goudkoff, *op. cit.*, 435–475, 1934.

[8] P. P. Goudkoff, *op. cit.*, 1934.

[9] R. D. Reed, personal communication.

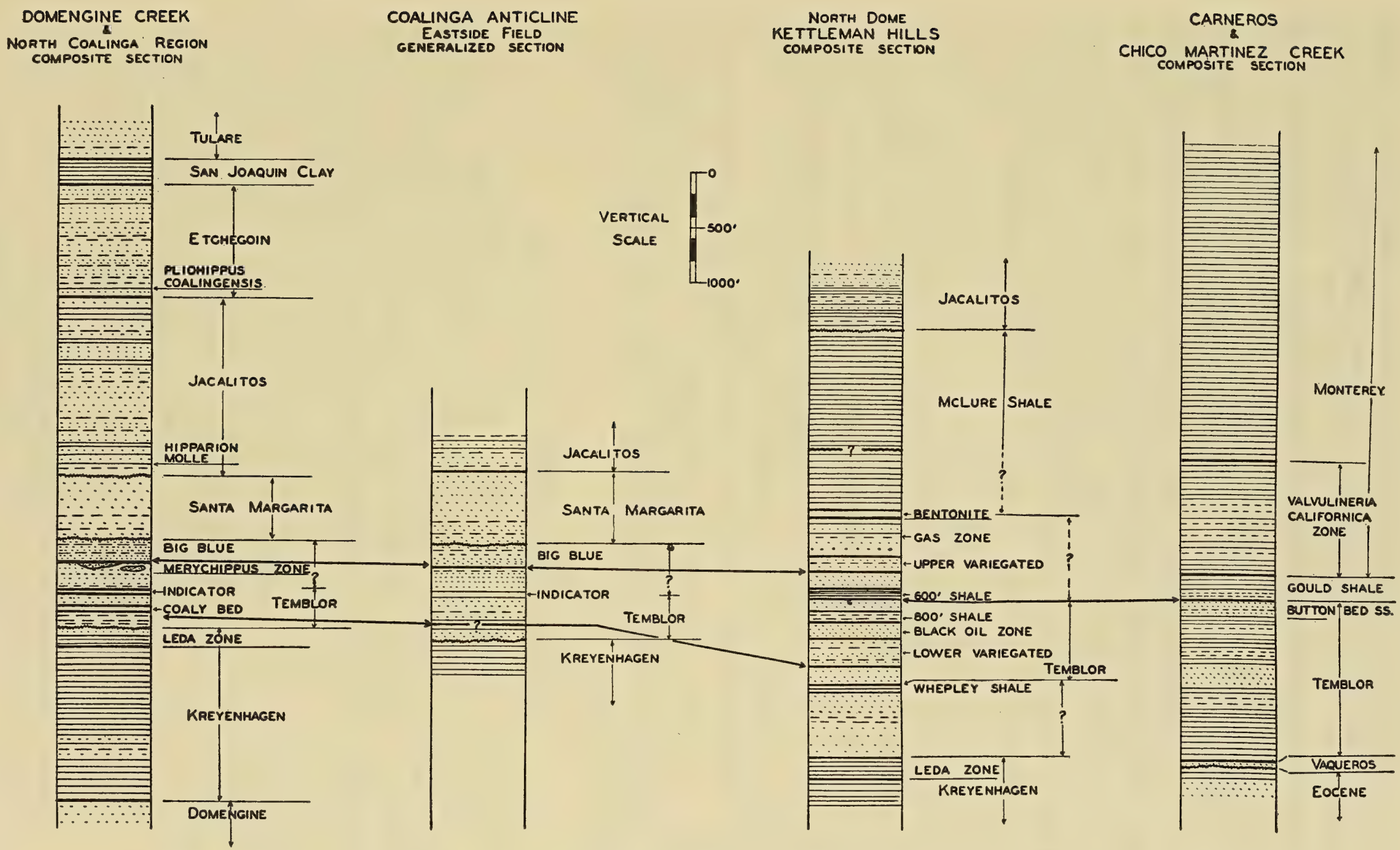

FIG. 3—Correlation chart showing position of Merychippus Zone in Tertiary section on Domengine Creek and its relation to a generalized section from Coalinga eastside oil field, a composite section from north dome of Kettleman Hills, composite section representing sequence of strata at type Temblor section on Carneros Creek and portion of Miocene section at Chico-Martinez Creek.

charts published by Gester and Galloway and Goudkoff.[1] There exists a rather general agreement that beds immediately or a short distance below the base of the "upper variegated" in the Kettleman Hills are equivalent to sandstones containing the Merychippus zone north of Coalinga.

Goudkoff[2] correlates the 600-foot shale in north dome Kettleman Hills sections with the Gould shale on Chico-Martinez Creek, and the sandstones equivalent to the Merychippus zone with the lower part of the *Valvulineria californica* zone on Chico-Martinez Creek. This correlation places the Merychippus zone in the early upper Miocene as defined by Goudkoff,[3] and higher than the top of the Button Bed sandstone on Carneros Creek, thus placing the Merychippus zone stratigraphically above the Temblor, as originally defined by F. M. Anderson.

Reed[4] regards the "Indicator Bed" on Domengine Creek as the correlative of the 600-foot shale in the North Dome sections of the Kettleman Hills. He concurs with Goudkoff's correlation of the 600-foot shale with the Gould shale on Carneros Creek, and believes that the horizon of the Merychippus zone should fall somewhere in the lower part of the *Valvulineria californica* zone on Carneros Creek which he considers to be late middle Miocene in age.

It is evident that the sandstones containing the Merychippus zone north of Coalinga are probably equivalent to beds lying above the Temblor at the type section, and that the use of the name "Temblor" with regard to the beds containing *Merychippus* on Domengine Creek is open to question.

AGE OF THE MERYCHIPPUS ZONE

As previously discussed, the Merychippus zone is in stage of evolution intermediate between the Mascall of eastern Oregon and the Barstow of the Mohave Desert, California. The Mascall has been regarded by vertebrate palæontologists as possessing a fauna typical of the middle Miocene. Chaney,[5] on the basis of evidence derived from fossil floras, has placed the age of the Mascall as middle or even upper Miocene. Simpson, in a recently published series of correlation charts,[6] places the Mascall in the early upper Miocene. One can conclude therefore that the Merychippus zone can not be older than late middle Miocene. In his description of the vertebrate faunas from the Mohave Desert, Merriam[7] assigned an uppermost Miocene age to the Barstow and referred the distinctly younger beds of the Ricardo to the lower Pliocene. Since these age determinations were made, Maxson[1] has found several of the horses peculiar to the Ricardo in beds of the Mint Canyon formation, which presumably underlies marine sediments of Cierbo or upper Miocene age. If the age determination of the marine horizon is essentially correct, this relationship tends to push the Barstow lower into the Miocene. The Barstow is distinctly closer in stage of evolution to the Merychippus zone than it is to the Ricardo. The position of the Merychippus zone can not then be assigned to a period of time younger than early upper Miocene.

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[1] G. C. Gester and John Galloway, *op. cit.*, 1169, 1933; P. P. Goudkoff, *op. cit.*, 465, 1934.

[2] P. P. Goudkoff, *op. cit.*, 456, 1934.

[3] P. P. Goudkoff, *ibid.*

[4] R. D. Reed, personal communication, Feb. 1935.

[5] R. W. Chaney, Carnegie Inst. Wash. Pub. No. 349, 48, 1925.

[6] G. G. Simpson, Bull. Amer. Mus. Nat. Hist., vol. 67, 87, 1933.

[7] J. C. Merriam, Univ. Calif. Pub., Bull. Dept. Geol., vol. 11, 454, 1919.

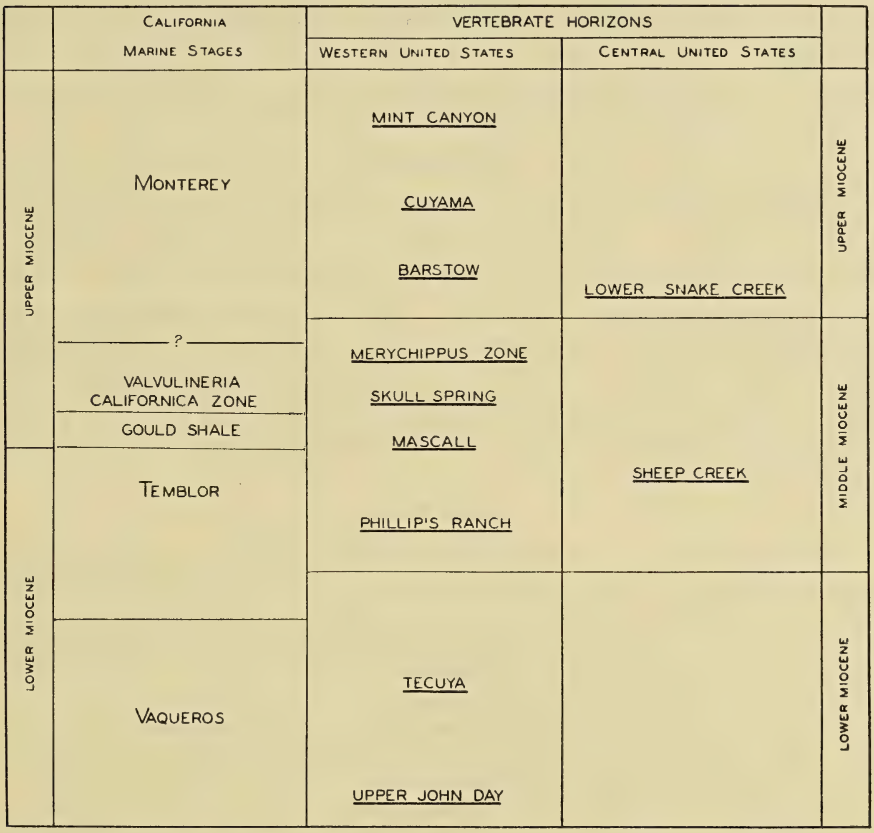

Fig. 4—Correlation chart suggesting time relationships of several Miocene Vertebrate horizons in Western United States to Miocene marine stages of California and to the Sheep Creek and lower Snake Creek horizons of Nebraska.

The correlation of the Merychippus zone on Domengine Creek with the *Valvulineria californica* zone has a distinct stratigraphic value, for the late middle Miocene or early upper Miocene age of the *Valvulineria californica* as determined by its invertebrate faunas indicates that, if the Miocene time scale as determined by the marine invertebrate faunas on the Pacific Coast is to remain essentially equivalent to that determined by means of continental vertebrate assemblages, the Mascall must be regarded as occupying a position very close to the exact middle of the Miocene and not in the upper third as has been recently suggested.

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[1] J. H. Maxson, Carnegie Inst. Wash. Pub. No. 404, 77–112, 1930.

Figure 4 is a correlation chart suggesting the stratigraphic relations of several vertebrate horizons to the Miocene Marine stages of California.

SYSTEMATIC DESCRIPTION OF FAUNA

Carnivora

The carnivore material from the Merychippus zone consists entirely of isolated teeth. With the exception of a single tooth, referable to *Hemicyon*, the specimens fall naturally into three group sizes. These groups are referred to *Tomarctus*, *Ælurodon* and *Amphicyon*. Unfortunately, the characters displayed by the carnassial teeth of members of the Canidæ are usually only of generic significance. Comparisons with known types emphasizes the fact that the present material is too incomplete to serve as a satisfactory basis for specific determinations.

Tomarctus sp.

The teeth of this small carnivore are referred without question to the genus *Tomarctus*. While a critical study of the relationships of *Tomarctus* Cope and *Tephrocyon* Merriam have not been attempted, there appears to be no reason why Matthew's[1] suggestion of generic identity of the two forms should not be accepted. In the following discussion the name *Tephrocyon* is regarded as a synonym of *Tomarctus*.

The material from the Merychippus zone consists of four upper carnassials (Nos. 1603, 1604, 1605, and 1606), two lower sectorial teeth (Nos. 1607 and 1608) lacking the anterior portions of the trigonids, the greater portion of an $M\underline{1}$ (No. 1609), and a single premolar (No. 1610) (Plate 2, figs. 1, 2, 4, and 5). In the superior carnassials the parastyle is a small cusp or elevation on the anterior ridge of the paracone. The protocone has been broken away on three of the specimens, but is present on the fourth (No. 1603). In this tooth the position of the protocone is anterior to that of the paracone and the cusp is rather small and low. A distinct cingulum is present on the external side of the metacone in all four teeth. The upper molar is rectangular in shape, the lingual side having approximately the same anteroposterior diameter as the external side. The paracone and metacone are low cusps connected by a slight ridge. The metaconule and protoconule are well developed. These cusps become connected at an early stage of wear and form an anteroposterior ridge across the middle of the tooth. The protocone is represented by a relatively heavy ridge, which runs across the entire lingual side of the tooth. In the two specimens presumably representing $M\overline{1}$, the entoconid and hypoconid are equally developed. When slightly worn these two cusps evidently form a transverse ridge with a small basin in front and a valley behind. In one of the teeth (No. 1608) the metaconid is distinctly larger than in the second specimen (No. 1607).

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[1] W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 50, 81–88, 1924.

In size and arrangement of cusps these teeth compare favorably with several of the species referred to *Tephrocyon* or *Tomarctus.* The teeth are smaller than in the type of *T. rurestris* (Condon) from the Mascall, and slightly larger than those of the specimen referred by Merriam to *T. temerarius* Leidy from the Barstow. *T. kelloggi* (Merriam) from the middle Miocene beds of Virgin Valley is a larger form. Compared to species from the Great Plains region the Coalinga specimens approach *T. optatus* Matthew more closely in size than they do any of the other known types. *T. brevirostris* Cope is larger and the type of *T. confertus* Matthew lacks the strong development of the proto- and metaconules seen in $M\underline{1}$ from the Merychippus zone. Apart from size differences there appears to be very little to distinguish the Coalinga species from most of the described forms. The material compares most favorably with *T. optatus* and may represent a species closely related to or identical with this form.

Ælurodon sp.

Four upper carnassials (Nos. 1611, 1612, 1613, and 1618), three of them complete, and three lower sectorial teeth (Nos. 1614, 1615, and 1617), one of which is perfectly preserved (No. 1615), are assigned to *Ælurodon* (Plate 2, figs. 6–9). In the upper teeth the parastyle is distinct, though small. The protocone is also small and occupies a position slightly anterior to that of the parastyle. The shearing blade is robust and heavy. In the lower teeth the metaconid is a distinct and well-developed cusp. The paraconid is smaller than the protoconid. The transverse diameter of the talonid region is smaller than that across the posterior side of the trigonid. The talonid possesses two cusps of which the hypoconid is the larger.

The superior carnassials are almost identical in size, shape and in arrangement of cusps with those of *Borophagus littoralis* Vander Hoof,[1] described from Santa Margarita beds near McKittrick, California. The lower jaw of this form is not known, and it is principally for this reason that the material from the Merychippus zone is not referred to *Borophagus.* The specimens from north Coalinga, although slightly smaller, agree also with upper teeth of *Borophagus cynoides* (Martin) from the Hemphill quarries, Texas. The lower teeth of the Texan species are distinguished by larger size of talonid, relative to the trigonid. However, this Pliocene species obviously represents an advance over forms from the Miocene. It seems possible that the lower teeth of the Coalinga form may represent an ancestral stage to the later hyænognathoid dogs. These specimens from the Merychippus zone are considerably larger than those of any species of *Tomarctus,* although the dental characters offer but little to distinguish them from that genus.

When compared with *Ælurodon wheelerianus* Cope, the teeth from north Coalinga appear to be quite similar. In fact, no clear distinctions can be made between the two types. The lower teeth are practically identical and the principal difference in the upper teeth is presented by the slightly smaller parastyle of the Coalinga specimens. Because of the agreement between the Coalinga form and *A. wheelerianus* in both upper and lower teeth and because the lower teeth of *B. littoralis* are unknown, the Coalinga material is referred to *Ælurodon.* However, the relative heaviness of the upper carnassials, coupled with the presence of a parastyle that is relatively smaller than in most

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[1] V. L. Vander Hoof, Univ. Calif. Pub., Bull. Dept. Geol. Sci., vol. 21, 15–24, 1931.

Ælurodons, is rather suggestive. In view of the late middle Miocene position of the Merychippus zone it may be possible that this material represents a form, larger although not otherwise clearly distinguishable from *Tomarctus*, and ancestral to either or both *Borophagus* and *Ælurodon*. The Coalinga type is considerably smaller than *A. haydeni* Leidy and the Ricardo form, *A. aphobus* Merriam.

Amphicyon sp.

Amphicyon is represented by two upper molars, an $M\underline{1}$ (No. 1619) and an $M\underline{2}$ (No. 1616), the trigonid and talonid portions of two lower carnassials (Nos. 1620 and 1621, respectively), a well-worn $M\overline{2}$ (No. 1622), a canine tooth (No. 1623) and a premolar (No. 1624) (Plate 2, figs. 11–14). $M\underline{2}$ (No. 1616) is a well-preserved tooth of the right side. In this tooth the paracone is more than twice as large as the metacone. The protoconule and metaconule are only slightly developed and form a small ridge on the internal occlusal surface. The protocone is a heavy ridge which runs across the entire lingual side and halfway up the posterior side of the tooth. The paracone has been lost from the $M\underline{1}$ (No. 1619). The metacone in this tooth was probably equal in size to the paracone. In this tooth the protoconule-metaconule ridge is well developed and encloses a distinct basin behind the paracone. The protocone has been damaged by abrasion and its exact form is therefore not represented.

In the lower carnassial fragments, the trigonid is considerably compressed in an anteroposterior direction. The metaconid is small and is essentially a part of the protoconid. The talonid is well worn; however, the hypoconid seems to have been the only important cusp, although some damage by abrasion has removed any indications of an entoconid if present. A well-worn $M\overline{2}$ (No. 1622) is also assigned to this genus. The characters of this tooth have been largely obliterated by wear; however, the tooth appears to have had two anterior cusps and a single posterior cusp as in *Amphicyon*. The antero-external corner of this tooth probably possessed a cusp sufficiently prominent to account for the small pocket worn in this area. This character was noted by Gazin[1] in a fragmentary $M\overline{2}$ referred to *A. sinapius* Matthew from the Skull Spring deposits of eastern Oregon. A small pocket worn on the postero-internal corner of the tooth may represent either a small entoconid or the worn surface may be due to an occlusion of the tooth with a cusp of an upper molar.

These teeth are smaller than those of *Amphicyon frendens* Matthew. The fragmentary material available compares favorably in size and in arrangement of cusps with *A. sinapius* from the Great Plains. This species has also been recognized in the Mascall fauna. It seems probable that the Coalinga specimens represent *A. sinapius*.

Hemicyon? sp.

A lower second molar (No. 1625) (Plate 2, fig. 10) from the Merychippus zone resembles closely the corresponding tooth of the type of *Hemicyon barstowensis* Frick[2] from the Barstow Miocene of the Mohave Desert, California. The cusps in this tooth are low and lack the trenchant character seen in *Amphicyon*. The tooth is still further distinguished from the latter genus in the more posterior position of the protoconid-metaconid ridge with reference to the anterior edge. Moreover, the hypoconid is a small low cusp, only slightly larger than the distinct entoconid. The exact relationships of the form characterized by this tooth are uncertain. However, the resemblances are more with *Hemicyon* than with any other genus. The tooth quite certainly does not belong to any of the described canid types from the Merychippus zone. In *Tomarctus*, *Ælurodon* and in *Borophagus* the anterior cusps of $M\bar{2}$ stand higher and have a considerably more trenchant character than in this tooth.

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[1] C. L. Gazin, Carnegie Inst. Wash. Pub. No. 418, 52, 1932.

[2] C. Frick, Bull. Amer. Mus. Nat. Hist., vol. 56, 28, 1926.

RODENTIA

Monosaulax sp.

Among the rodents only the beaver group is recorded in the collections. A single cheek-tooth (No. 496) and a fragment of a ramus (No. 653) with two teeth were referred to this castorid genus by R. A. Stirton[1] of the University of California. This genus has been recognized by Mr. Stirton in the Miocene of the Great Plains and in the Cedar Mountain fauna of Nevada.

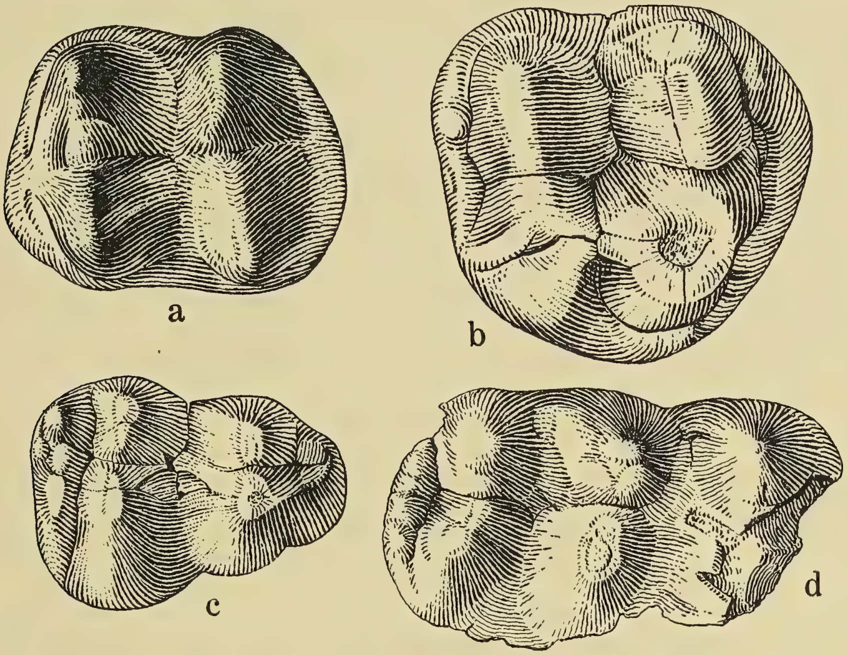

FIG. 5—*Miomastodon* or *Trilophodon* ? sp. a, deciduous premolar, No. 1628; b, $P\underline{4}$, No. 1630; c, deciduous premolar, No. 1629; d, $M\underline{1}$?, No. 1633. Calif. Inst. Tech. Coll., Merychippus Zone North Coalinga district, California; x 1.

PROBOSCIDEA

Miomastodon or Trilophodon? sp.

The proboscidean material in the collections consists of the following specimens: Four deciduous premolars (Nos. 1626, 1627, 1628, and 1629), three fourth upper premolars (Nos. 1630, 1631, and 1632), an upper $M\underline{1}$? (No. 1633), a partially complete $M\underline{2}$? (No. 1634), and a number of miscellaneous tooth fragments. Four of these specimens are illustrated in figure 5.

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[1] R. A. Stirton, personal communication.

No tusk or skeletal materials were found during the course of the excavations. The milk teeth and the permanent premolars possess four cusps, with each cusp remaining distinct and isolated until the tooth is worn almost to the base of the crown. Very few secondary cusps are present and these are extremely small, being minor tubercles situated between the major cusps near the base of the crown. On several teeth the enamel of the four cusps is perfectly smooth. The crown of the first molar, No. 1633, possesses three rows of two cusps each, although the individuality of the cusps disappears with wear. The partially complete $M\underline{2}$? (No. 1634) is considerably larger than $M\underline{1}$ but is otherwise essentially similar.

No. 1634 compares favorably with the type of *Miomastodon merriami* Osborn from the Virgin Valley beds of northwestern Nevada. In 1915 Merriam[1] tentatively assigned a milk molar and a fragment of a permanent molar from the Merychippus zone to *Tetrabelodon*. While the present material offers little in contradiction to Merriam's determination, the mastodont genera now recognized in the middle Miocene are *Miomastodon* and *Trilphodon*. Satisfactory generic determination can not be made, however, on the basis of available specimens from the Merychippus zone. Mr. E. H. Colbert[2] of the American Museum of Natural History, who has examined the materials, has kindly made the following comment: "I believe the choice narrows down to *Miomastodon* or *Trilophodon*. It is pretty difficult to be definite." It is interesting to note, however, that the relationships of the Coalinga form appear to be with the more primitive members of the Proboscidea found in North America. Absence of representatives of the group on this continent prior to middle Miocene time may furnish a basis for regarding the presence of these primitive forms in California as an indication of a near middle Miocene age for the Merychippus zone.

Perissodactyla

Among the Equidæ five species have been recognized three anchitheriine genera, *Hypohippus*, *Archæohippus* and *Parahippus*, and two species of *Merychippus*. The major part of the collection consists of isolated teeth referable to the species *Merychippus californicus*, the type specimen of which was described by Merriam from this locality. The remaining species are represented by considerably smaller numbers of specimens. The Equidæ are of particular interest in that they clearly demonstrate the intermediate position of the Merychippus zone with respect to the Mascall and the Barstow. Three of the species, *Hypohippus*, *Parahippus* and *Merychippus brevidontus* are found in the Mascall and in other middle Miocene horizons of eastern Oregon and northwestern Nevada, while the *Archæohippus* is unquestionably a Barstow species. The material determined as *Merychippus californicus* includes teeth that show close resemblance to specimens from the Barstow and the Mascall. The Equidæ from the Merychippus zone have been described in detail in two previous papers by the writer.[3] A résumé of these descriptions are included in the present paper.

Hypohippus sp.

An upper molar (No. 885) and three lower premolars (Nos. 886, 887 and 888) belong to the genus *Hypohippus*. The material is unfortunately inadequate for more than a generic determination. The Coalinga specimens are considerably smaller than the few teeth described as *Hypohippus* near *affinus* (Leidy) by Merriam from the Barstow, and they are unquestionably specifically separable from this form. *Hypohippus* has not been recorded from the Mascall. *Hypohippus* near *osborni* Gidley from the Virgin Valley beds is similar in most respects though somewhat larger than teeth from the Merychippus zone. The relationships of the north Coalinga form as based upon these teeth seem rather to be with the Virgin Valley form than with the *Hypohippus* from the Barstow.

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[1] J. C. Merriam, *op. cit.*, 13, 1915.

[2] E. H. Colbert, personal communication to Dr. Chester Stock.

[3] F. D. Bode, Carnegie Inst. Wash. Pub. No. 440, art. V, 1933; Carnegie Inst. Wash. Pub. No. 453, art. V, 1934.

Archæohippus mourningi (Merriam)

Following *Merychippus*, *Archæohippus* is one of the more commonly occurring forms in the collections from the Merychippus zone. To this genus have been assigned over fifty upper and lower cheek-teeth and a well-preserved ramus with P$\overline{3}$–M$\overline{3}$ (No. 484). *Archæohippus mourningi*, with higher-crowned cheek-teeth, from the north Coalinga locality, is a decidedly more advanced type than *Archæohippus ultimus* (Cope) from the Mascall. In *A. ultimus* the hypostyle consists of a single cusp, while in the Coalinga teeth this structure is triangular in shape and encloses a small fossette. M$\underline{3}$ in the type of *A. ultimus* is not reduced in size. On the other hand, the upper third molars of *Archæohippus* from the Merychippus zone show considerable reduction when compared to the two preceding molars. In the Coalinga teeth the protocone and hypocone widen toward their base to an extent which considerably obstructs the opening of the valley between protoloph and metaloph. In the Mascall form this valley is widely open and the two internal cusps are smaller. None of the teeth from the Merychippus zone exhibits the heavy internal cingulum seen in the type of the Mascall species.

The teeth from the Merychippus zone agree in almost all respects with the type and paratype of *A. mourningi* (Merriam) from the Barstow. The only noticeable difference appears to be the absence of an external cingulum on lower teeth of the paratype. This character varies considerably in the large collection of teeth from the Merychippus zone and appears to have no diagnostic value. The Coalinga material is referred unquestionably to *A. mourningi* and is clearly distinct from the Mascall species.

Parahippus brevidens Marsh

Parahippus is represented in the collections by some twenty well-preserved upper and lower cheek-teeth. That the material should be assigned to a progressive parahippine form is indicated by the relatively high crowns, abundant cement, and progressive character of the ptychoid crenulations of the walls of the metaloph. These features serve to isolate the Coalinga form from most of the species of *Parahippus*. In development of the crenulations on the walls of the metaloph, the teeth from the Merychippus zone agree closely with *Parahippus crenidens* Scott. They differ from *P. crenidens*, however, in their less strongly developed ectoloph, shape of protoloph and heavy coating of cement. The deciduous teeth of *Parahippus cognatus*, while similar in some characters, represent a much larger horse. Comparisons with this form are inadequate, since no milk teeth of *Parahippus* have been recognized in the collections from the Merychippus zone.

Several teeth in the collections of the California Institute of Technology from the Mascall and referred to *Parahippus brevidens* Marsh are practically identical with the *Parahippus* teeth from North Coalinga. A comparison with the type of *P. brevidens* as well as with the topotype material fails to disclose any characters which may serve to separate the Coalinga form from this species. *Parahippus* has not been recorded from the Barstow nor, so far as the writer is aware, from any Miocene horizon as late in age as the Barstow. The presence of *Parahippus* may therefore have some significance in pointing toward a close time relationship between the faunas from the Merychippus zone and the Mascall.

Merychippus brevidontus Bode

This species is known by approximately seventy-five upper and lower cheek-teeth. The specimens, although representing fully hypsodont teeth, possess exceptionally low crowns and exhibit extreme complexity of the enamel pattern. The characters seen in these teeth do not intergrade with those of the larger and more abundant species, *M. californicus*, and were employed therefore in the recognition of a new specific type. Teeth referable to this species are relatively abundant in middle Miocene collections from eastern Oregon and northwestern Nevada. Teeth similar to *M. brevidontus* are absent in the Barstow and related upper Miocene horizons. A detailed description of *M. brevidontus* has been given in a previous paper.[1]

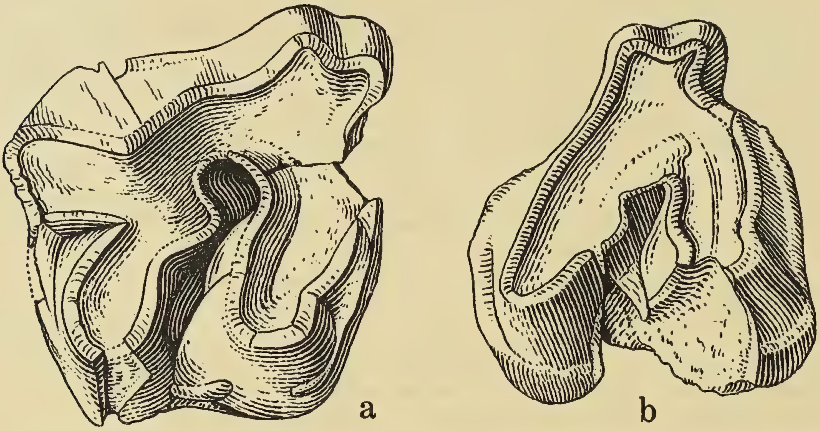

Fig. 6—Rhinocerotid cf. *Aphelops*. a, upper cheek-tooth, No. 1639; b, $\mathrm{M}\underline{3}$, No. 1744. Calif. Inst. Tech. Coll., Merychippus Zone, North Coalinga district, California; x 1.

Merychippus californicus Merriam

The Merychippus zone derives its name from the abundant representation of this species in the north Coalinga horizon. Cheek-teeth of *Merychippus californicus* comprise nearly half of all the specimens collected from this zone.

The degree of variation of the cheek-tooth characters as seen in this collection makes it difficult to determine the exact affinities of this species. The average grouping of characters seems to be generally distinct from the average grouping of characters seen in similar large collections from other horizons. Individual teeth can frequently be assigned to any one of several species of this genus from North American Miocene horizons. In general, the variations more frequently represented are those which would include *Merychippus isonesus* (Cope) from the Mascall and *M. sumani* Merriam from the Barstow. A fuller discussion of the characters and relationships of *M. californicus* has been given in a previous paper.[2]

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[1] F. D. Bode, Carnegie Inst. Wash. Pub. No. 453, art. V, 42–43, 1934.

[2] F. D. Bode, *Ibid.*, 43–47, 1934.

Rhinocerotid cf. Aphelops

Some fifteen teeth in the collections are referable to the Rhinocerotidæ. A generic determination is questionable. However, the brachydont character of the dentition tends to affiliate this form with *Aphelops* rather than with *Teleoceras*. The teeth show a slight development of the crochet and ante-crochet. The two features of the enamel pattern were not found associated in a single tooth. Two tarsal elements (Nos. 1636 and 1637) are also present in the collections. These elements resemble those of *Aphelops* more closely than they do *Teleoceras* and may afford corroborative evidence for the present determination.

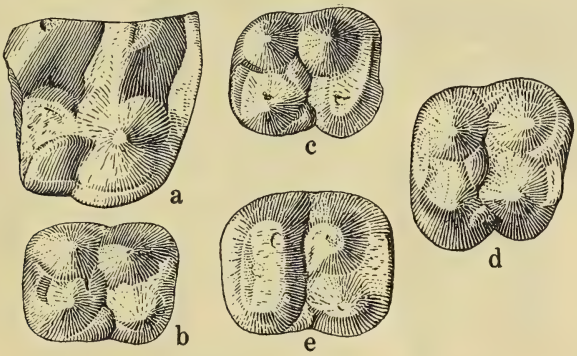

Fig. 7—*Prosthennops?* sp. a, Dp $\underline{4}$, No. 1638; b to e, isolated cheek-teeth, Nos. 1745, 1746, 1747, and 1748 inclusive. Calif. Inst. Tech. Coll., Merychippus Zone, North Coalinga district, California. x 1½.

ARTIODACTYLA

Prosthennops? sp.

A dicotyline form previously known by a few teeth is represented in the collections by fifteen upper and lower molars and premolars. Definite generic determination of the form on the basis of this material is not trustworthy, but certain characters of the premolars are suggestive of *Prosthennops*. The four-cusped arrangement, on the occlusal surface in the premolars, in contradistinction to a fewer number of cusps seen in species of *Desmathyus* and the tendency of the four cusps to remain distinct rather than to develop into cross-crests as in *Platgyonus* are characters in which the Coalinga genus resembles *Prosthennops*. A deciduous fourth premolar (No. 1638) (fig. 7a) and two specimens assigned to Dp$\underline{3}$ (Nos. 1639 and 1640) are similar to corresponding teeth in the type of *Desmathyus validus* Matthew. The permanent teeth are bunodont with a tendency to become multi-cuspid, which distinguishes them from teeth of *Platygonus* in which the cusps are simpler, higher and fused into cross-crests. Several astragali in the collection are also referred to this form. These specimens are approximately comparable in size to similar elements in the Barstow collections.

Camelidæ

The collections from the Merychippus zone contain nearly one hundred teeth referable to the Camelidæ. These teeth do not fall into any distinctive groups according to size but appear to be gradational in this character from the smallest to the largest. The dentition is brachydont. In addition to the teeth, however, the collection contains a representation of carpal and tarsal elements. Within this collection there appear to be three types of sizes represented, although specimens intermediate in size between those of individual groups are not lacking.

The characters displayed by the cheek-teeth, as for example size and strength of the external styles, have little value in attempting to make a generic determination. Most of the skeletal material has suffered considerably from abrasion. As a result, the diagnostic characters are for the most part

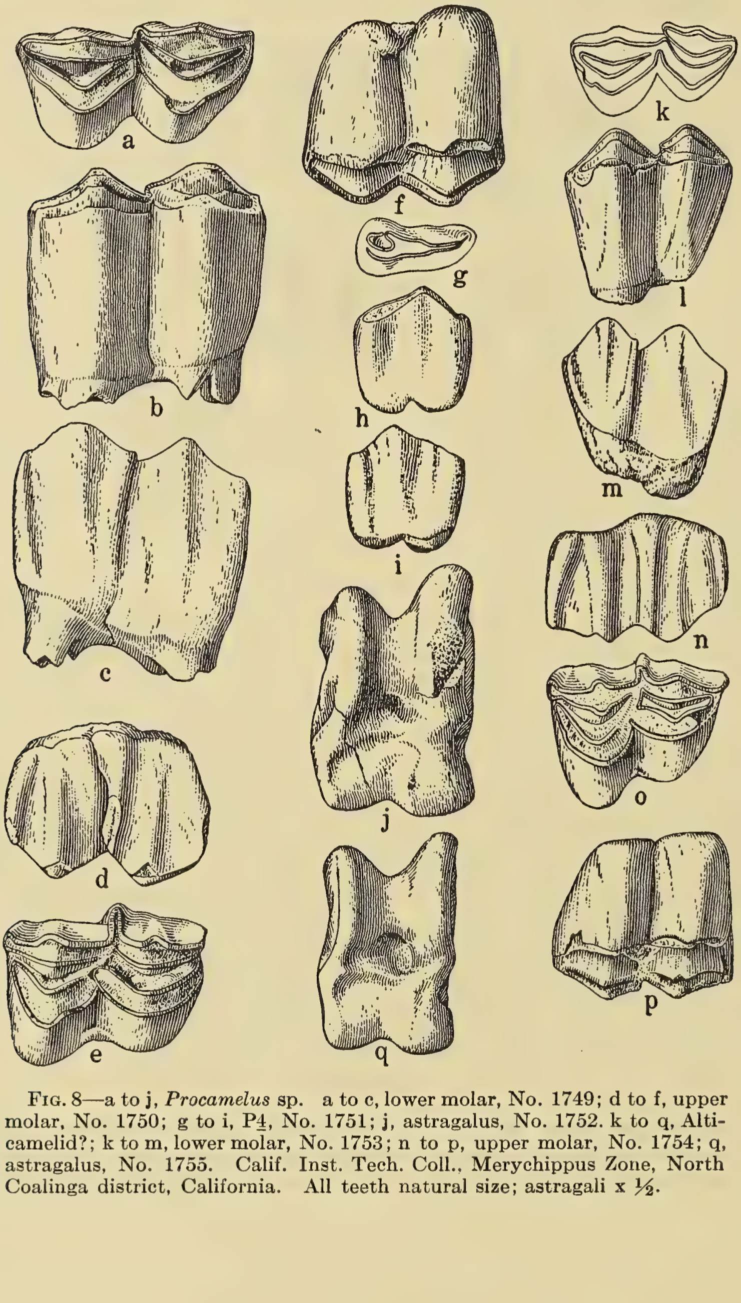

FIG. 8—a to j, *Procamelus* sp. a to c, lower molar, No. 1749; d to f, upper molar, No. 1750; g to i, P4, No. 1751; j, astragalus, No. 1752. k to q, Alticamelid?; k to m, lower molar, No. 1753; n to p, upper molar, No. 1754; q, astragalus, No. 1755. Calif. Inst. Tech. Coll., Merychippus Zone, North Coalinga district, California. All teeth natural size; astragali x ½.

but poorly defined. The astragali offer perhaps the best basis for the grouping of the forms. The larger astragali are comparable in size to those from the Barstow referred by Merriam to *Procamelus*. The larger premolars in the collection are of a size nearly comparable to that seen in average specimens of species of this genus. The larger cheek-teeth present no characters which would serve to separate them from *Procamelus*. In view of the relative abundance of specimens representing this genus in most upper Miocene collections, it seems reasonable to suppose that these very similar teeth from the Merychippus zone represent *Procamelus*.

The second form has been recognized largely by the characters of the astragali. Approximately fifteen of these elements in the collection, slightly smaller in size than the material referred to *Procamelus*, are distinguished from the latter by their narrowness. These narrow astragali may represent an alticamelid in the collections. To this type has been assigned teeth which seem to occupy also an intermediate size position. The narrow astragali certainly indicate the presence of a form differing specifically from that known by the material referred to *Procamelus* and the smallest camelid. The group of smaller forms compares in size and in structure of cheek-teeth to some undescribed specimens of *Miolabis californicus* Maxson from the Mint Canyon beds of California. It appears possible that the small teeth and limb elements in the collection from the Merychippus zone may belong to this genus.

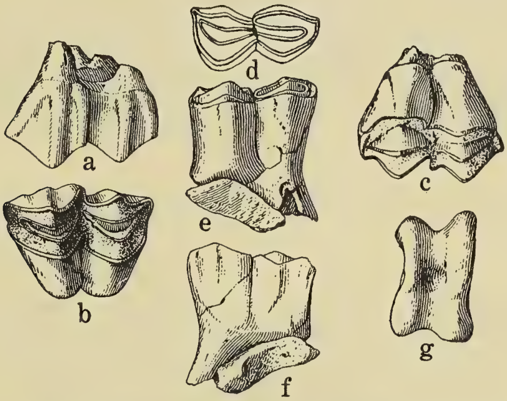

FIG. 9—Small camelid, possibly *Miolabis*. a to c, upper molar, No. 1756; d to f, lower molar, No. 1757; g, astragalus, No. 1758. Calif. Inst. Tech. Coll., Merychippus Zone, North Coalinga district, California. Teeth natural size, astragalus x ½.

Pliauchenia and *Protolabis* differ from the types recorded in the present collection in larger size and hypsodont cheek-teeth.

Blastomeryx (Dyseomeryx) sp.

One upper (No. 1641) and four lower molars (Nos. 1642, 1643, 1644, and 1645), a third or fourth lower premolar (No. 1646) and two deciduous upper molars (Nos. 1647 and 1648) together with several astragali are referred to *Dyseomeryx* Matthew, known from the Sheep Creek beds of western Nebraska. All of the teeth are short-crowned and are thus excluded from the genus

Merycodus. The metaselene and protoselene of the milk teeth (Nos. 1647, 1648) remain isolated throughout most of the wear of the tooth. These crescents are connected to the ectoselene in the permanent molar, but are apparently not joined together until a late stage of wear. In $M\overline{3}$ (No. 1642) the internal talonid cusp is more or less completely united with the hypoconid, as in *D. riparius* Matthew. There is practically no indication of a basal cusp between the outer crescents of the lower molars. An anterior basal cingulum is but slightly developed on these teeth. The development of the cross-crests in $P\overline{3}$ or $P\overline{4}$ (No. 1646) is similar to that found in many of the species of *Blastomeryx.* This specimen is somewhat larger than in the ramus of *D. riparius*, illustrated by Matthew.[1] The median transverse crest is expanded internally with an incipient pillar developing from the postero-internal side of the main pillar. The remaining crests have a simple rectilinear appearance. The astragali are small but present no other distinguishing characteristics.

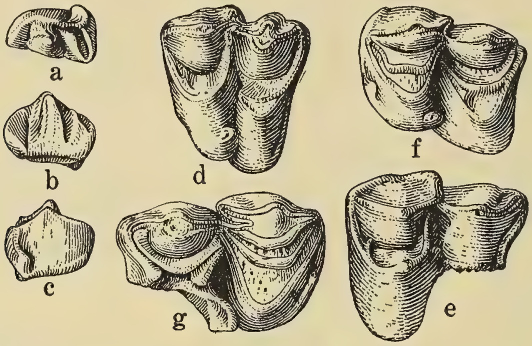

FIG. 10—*Blastomeryx* (*Dyseomeryx*) sp. a to c, $P\overline{4}$ or $P\overline{3}$, No. 1646; d to e, $Dp\underline{4}$? Nos. 1647 and 1648 incl.; f and g, lower molars, Nos. 1643 and 1644 incl. Calif. Inst. Tech. Coll., Merychippus Zone, North Coalinga district, California. Figs. a to c, x 1; figs. d to g, x 1½.

The character of brachydonty excludes this form from *Merycodus.* Compared to teeth in species of *Blastomeryx*, the Coalinga specimens are considerably larger. The latter are almost identical in appearance to *Blastomeryx* (*Dyseomeryx*) *riparius* Matthew from the Sheep Creek beds of western Nebraska. This subgenus was erected by Matthew to include large species otherwise referred to *Blastomeryx.* The enamel walls of the teeth are slightly rugose, but this character is not so well developed as in *Dromomeryx.*

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[1] W. D. Matthew, Bull. Amer. Mus. Nat. Hist., vol. 50, 196–199, 1924.

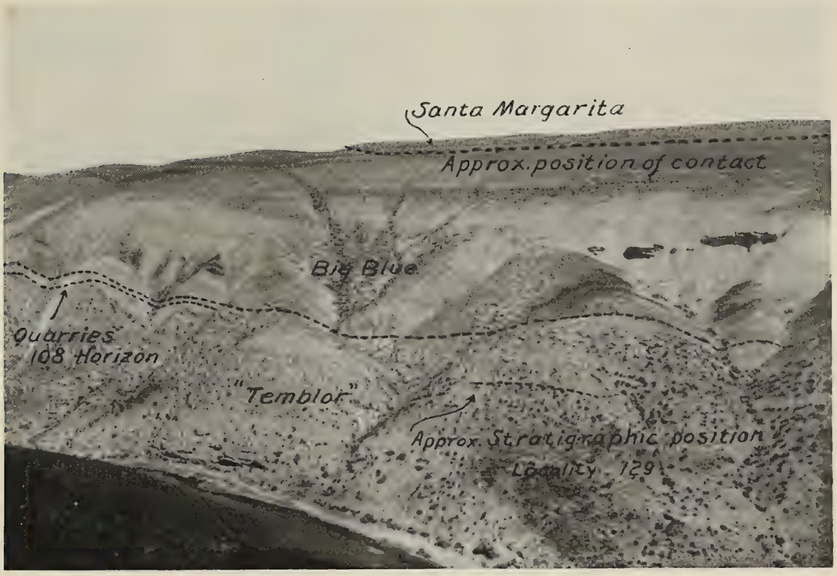

Santa Margarita
Approx. position of contact
Big Blue
Quarries 108 Horizon
"Temblor"
Approx. Stratigraphic position Locality 129

Fig. 1—View of geologic section on Domengine Creek from the west, showing approximate position of "Temblor," Big Blue, and Santa Margarita contacts, and stratigraphic position of Calif. Inst. Tech. localities 108 and 129. Merychippus zone, North Coalinga district, California.

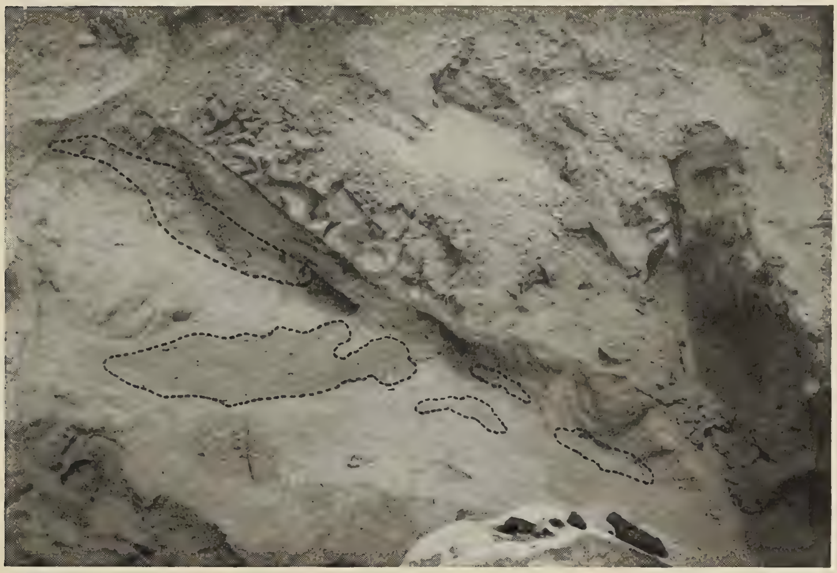


Fig. 2—View of quarry wall in Merychippus zone at Calif. Inst. Tech. locality 129. Pebble conglomerate lenses containing fossil material are outlined in dotted lines.

PLATE 2

FIGS. 1 and 2—*Tomarctus* sp. Figure 1, $P\underline{4}$, No. 1603; figure 2, $M\underline{1}$, No. 1601.

FIG. 3—*Amphicyon* sp., talonid of $M\overline{1}$, No. 1621.

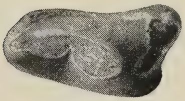
FIGS. 4–5a—*Tomarctus* sp. Figure 4, $M\overline{1}$, No. 1607; figure 5 and 5a, $M\overline{1}$, No. 1608.

FIGS. 6–9a—*Ælurodon* sp. Figures 6 and 6a, $P\underline{4}$, No. 1613; figures 7 and 7a, $M\overline{1}$, No. 1614; figures 8 and 8a, $M\overline{1}$, No. 1615; figures 9 and 9a, $P\underline{4}$, No. 1611.

FIGS. 10–10a—*Hemicyon?* sp., $M\overline{2}$, No. 1625.

FIGS. 11–14a—*Amphicyon* sp. Figures 11 and 11a, $M\overline{2}$, No. 1622; figure 12, $M\underline{2}$, No. 1616; figure 13, $M\underline{1}$ with paracone restored, No. 1619; figures 14, 14a, trigonid of $M\overline{1}$, No. 1620.

All specimens from Calif. Inst. Tech. Collections, Merychippus zone, North Coalinga district, California; x ¾.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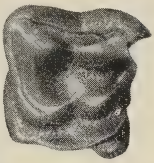
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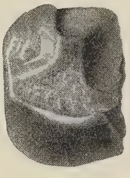
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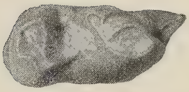
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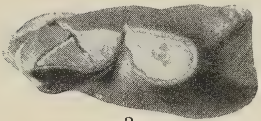
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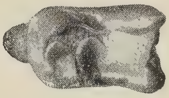
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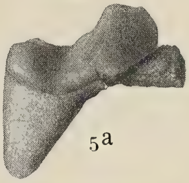
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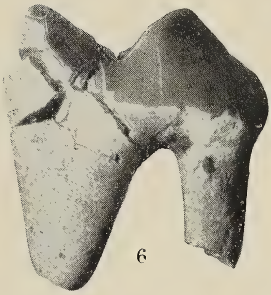
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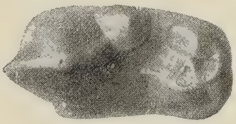
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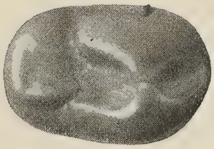
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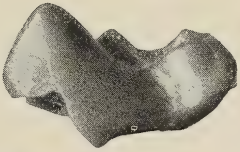
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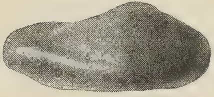
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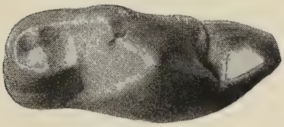
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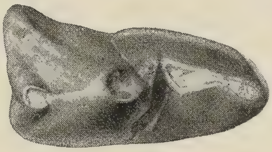
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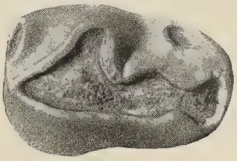
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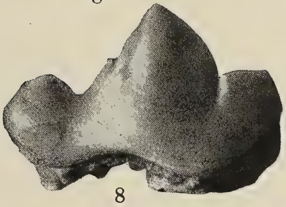
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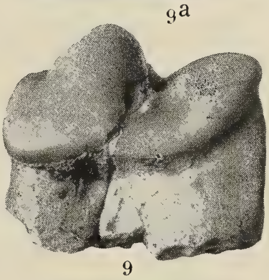
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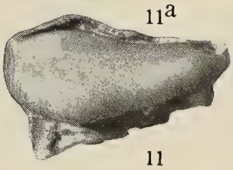
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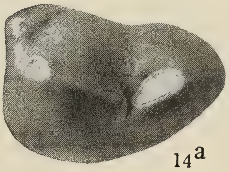
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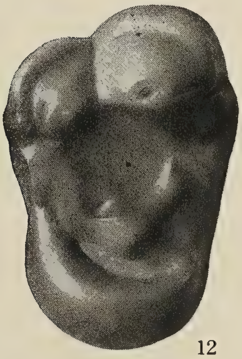
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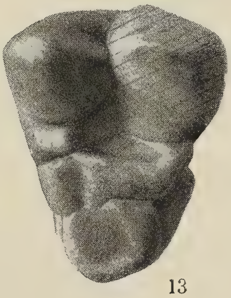
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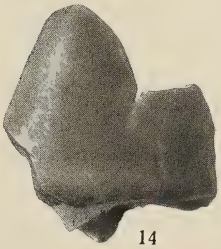
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CONTRIBUTIONS TO PALÆONTOLOGY

VII

A MIOCENE MAMMALIAN FAUNA FROM SUCKER CREEK, SOUTHEASTERN OREGON

By David W. Scharf

With two plates and eleven text-figures

[Issued July 20, 1935]

CONTENTS

Page
Introduction 99
Sucker Creek Fauna 101
Environment of Fauna 101
Age and Relationships of Fauna 102
Systematic Description 104
    Carnivora 104
        Canid (?) sp. 104
    Rodentia 104
        Sciurid (?) sp. 104
        Chalicomyid sp. 104
        Mylagaulus cf. lævis Matthew 104
    Proboscidea 105
        Mastodont sp. 105
    Perissodactyla 105
        Hypohippus near osborni Gidley 105
        Parahippus avus (Marsh) 105
        Merychippus Leidy 106
        Merychippus isonesus (Cope) 107
        Merychippus brevidontus Bode 108
        Rhinocerotid sp. 109
        Moropus sp. 109
    Artiodactyla 110
        Prosthennops (?) sp. 110
        Ticholeptus sp. 111
        Merychyus (?) sp. 114
        Dromomeryx near borealis (Cope) 115
        Merycodus cf. nevadensis Merriam 116
        Camelid (?) sp. a 117
        Camelid (?) sp. b 118

A MIOCENE MAMMALIAN FAUNA FROM SUCKER CREEK, SOUTHEASTERN OREGON

INTRODUCTION

Sediments occurring along the lower course of Sucker Creek,[1] in eastern Malheur County, Oregon, have been correlated with the Payette formation of southwestern Idaho on the basis of fossil plant remains found in them. A fossil mammalian fauna, collected from the Sucker Creek beds by field parties of the California Institute, now makes possible a clearer understanding of the relationships between the Miocene mammalian stages found in the northern Great Basin Province and the Payette stage of southwestern Idaho. Because of its incompleteness, the Payette mammalian assemblage up to the present time has furnished no thoroughly satisfactory basis for comparison with similar faunas occurring farther to the west.

The Payette formation, occurring in the region drained by the lower course of the Snake River, was named by Waldemar Lindgren in 1898.[2] The flora has been described by F. H. Knowlton[3] and more recently by R. W. Chaney.[4] The age of the Payette has been determined chiefly by plant remains. In support of a Miocene age for this plant assemblage Chaney makes the following statement: "The position of the Payette formation, above basalt lavas, is in accord with the relation of the Miocene Mascall formation to the Columbia lavas in Oregon. Vertebrate remains collected from the Payette formation by Buwalda are referred by him to the Middle or Upper Miocene. There appears, therefore, to be an agreement between the evidence of the flora, the fauna and the stratigraphy in pointing toward the Miocene age of the Payette formation." [5]

Future geologic mapping may show that the Sucker Creek beds are an integral part of the Payette formation. That the Sucker Creek beds are directly related in age to the Payette is shown by the flora, and such comparisons as can be made between the fossil mammals obtained at Sucker Creek and those from the type section of the Payette are fully in accord with this view. Buwalda[6] reports the presence in the Payette beds of Idaho of a fauna which includes a mastodont, *Hypohippus*, a rhinocerotid, *Merycodus*, and a camelid.

Approximately forty miles west of the Sucker Creek deposits is the Skull Spring occurrence. The beds of that name have yielded a large and varied mammalian assemblage described by C. L. Gazin.[1] Gazin assigns a Middle Miocene age to the fauna, correlating it with the Mascall of north-central Oregon and with the Virgin Valley of northwestern Nevada. The sediments carrying the fossils were correlated with the Payette formation.

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[1] On many maps this creek is called Succor Creek. Since the present spelling of the name is that recorded on recent road maps, it is adopted in this paper.

[2] W. Lindgren, 18th Ann. Report U. S. Geol. Surv., Pt. 3, 632–634, 1898.

[3] F. H. Knowlton, 18th Ann. Report U. S. Geol. Surv., Pt. 3, 721–744, 1898.

[4] R. W. Chaney, Amer. Jour. Sci., ser. 5, vol. 4, 214–222, 1922.

[5] R. W. Chaney, *ibid.*, 220, 1922.

[6] J. P. Buwalda, Science, n.s., vol. 60, 572–573, 1924.

The more important collecting localities in the Sucker Creek beds occur approximately nine miles north of Rockville, Oregon, and approximately five miles west of the Oregon-Idaho border. Location of the beds is shown on the accompanying map (fig. 1).

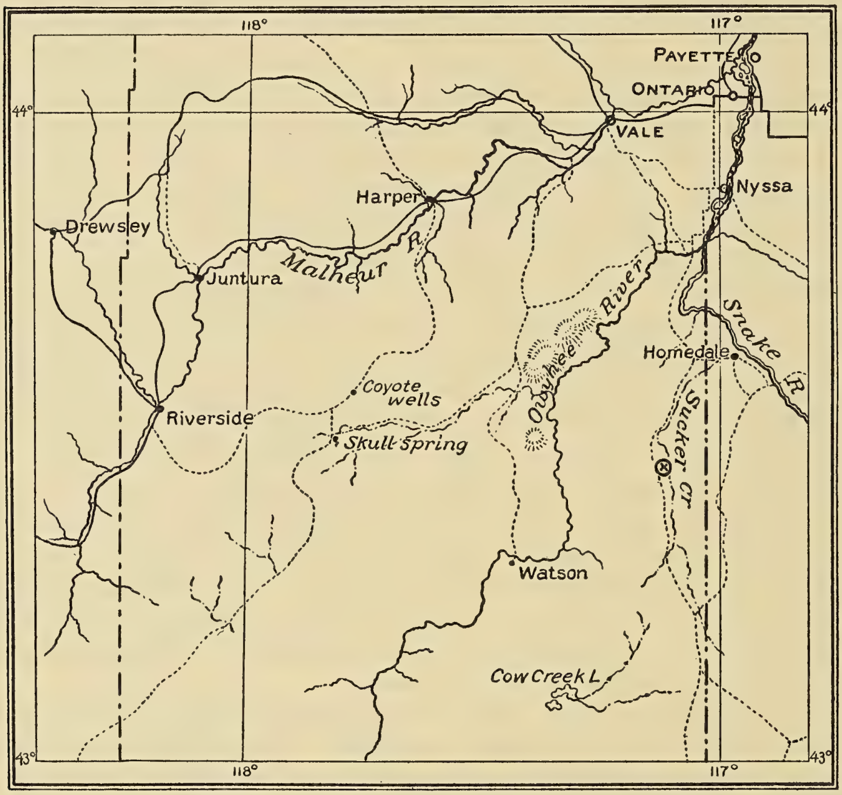

FIG. 1—Index map of portion of eastern Oregon and adjacent region of western Idaho, showing location (X) of Sucker Creek fossil vertebrate occurrence.

The beds carrying the fossils consist of fine- to medium-grained pyroclastics, varying from white to green and brown in color. Presence of fish vertebræ and of ostracod shells indicates deposition of at least a portion of the sediments in a body of water.

Fossil mammalian remains were first discovered in the Sucker Creek beds by Chester Stock and E. L. Furlong in 1927. The writer is indebted to Dr. Stock for the opportunity to undertake this study and for kindly advice and criticism during its progress. The illustrations were prepared by Mr. John L. Ridgway.

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[1] C. L. Gazin, Carnegie Inst. Wash. Pub. No. 418, 37–86, 1932.

SUCKER CREEK FAUNA

While the mammalian collections from Sucker Creek are rather fragmentary and incomplete, nevertheless sufficient material is available to permit certain reasonably trustworthy conclusions. Continued collecting in the Sucker Creek region doubtless will give a fuller representation than is now known of the fauna which inhabited the region at the time the beds were deposited.

The following is a list of the forms recognized in the present collection:

- Carnivora
    - Canid (?) sp.
- Rodentia
    - Sciurid (?) sp.
    - Chalicomyid sp.
    - Mylagaulus cf. lævis Matthew
- Proboscidea
    - Mastodont sp.
- Perissodactyla
    - Hypohippus near osborni Gidley
    - Parahippus avus (Marsh)
    - Merychippus isonesus (Cope)
    - Merychippus brevidontus Bode
    - Rhinocerotid sp.
    - Moropus sp.
- Artiodactyla
    - Prosthennops (?) sp.
    - Ticholeptus sp.
    - Dromomeryx near borealis (Cope)
    - Merycodus cf. nevadensis Merriam
    - Camelid (?) sp. a
    - Camelid (?) sp. b

ENVIRONMENT OF FAUNA

Although the vertebrate fossil record is fragmentary, certain suggestions are indicated as to the environmental conditions that prevailed in the region during the period of deposition of the Sucker Creek sediments. The brachydont ungulates represented by *Hypohippus*, *Parahippus*, *Moropus* and *Dromomeryx* were evidently browsing types and their presence suggests a glade or forest environment, with a humidity greater than that of the semiarid desert which characterizes the region today. On the other hand, the occurrence of hypsodont grazing forms, as for example *Merychippus* and *Merycodus*, may well suggest an association of extensive grasslands with the forest areas.

The conclusions as to the environment indicated by the Payette flora, derived by Chaney, are in accord with the evidence offered by the brachydont, browsing ungulates. Chaney considers the climate to have been similar to that of northern California and southwestern Oregon today. A forested region of some relief is indicated, with oaks as the dominant form on the slopes, while the lake or stream borders were swampy.[1]

AGE AND RELATIONSHIPS OF FAUNA

In the light of the known Tertiary faunal stages for western North America the assemblage from Sucker Creek is certainly of Miocene age. Presence of the species *Merychippus isonesus*, *Dromomeryx* near *borealis*, and *Mylagaulus* cf. *lævis*, found in Middle Miocene faunas elsewhere, would seem to suggest a nearly comparable age for the Sucker Creek assemblage. *Hypohippus*, *Parahippus* and *Moropus* are unfortunately too incomplete for specific determination, but may be indicative likewise of this stage.

The mammalian assemblage most closely related to the Sucker Creek fauna in time and in geographic position is that reported from the region of Skull Spring by Gazin.[2] The similarity between the two faunas is at once apparent from a comparison of the faunal lists given below:

Sucker Creek	Skull Spring
Carnivora	Carnivora
	Tomarctus cf. brevirostris Cope
	Euoplocyon (?) sp.
Canid (?) sp.	Canid (?) sp.
	Amphicyon sinapius Matthew
	Amphicyon cf. frendens Matthew
	cf. Pliocyon medius Matthew
	Hemicyon n. sp.
	Martes (Tomictis) gazini Hall
Rodentia	Rodentia
Sciurid (?) sp.	Sciurus malheurensis Gazin
	Sciurus tephrus Gazin
	Citellus longirostris Gazin
	Liodontia alexandræ (Furlong)
Mylagaulus cf. lævis Matthew	Mylagaulus cf. lævis Matthew
	Diprionomys (?) oregonensis Gazin
Chalicomyid sp.	

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[1] R. W. Chaney, *op. cit.*, 221–222, 1922.

[2] C. L. Gazin, *op. cit.*, 37–86, 1932.

SUCKER CREEK	SKULL SPRING
Proboscidea	Proboscidea
Mastodont sp.	Mastodont sp.
Perissodactyla	Perissodactyla
Hypohippus near osborni Gidley	Hypohippus sp.
Parahippus avus (Marsh)	Parahippus near coloradensis Gidley
Merychippus isonesus (Cope)	Merychippus isonesus (Cope)
Merychippus brevidontus Bode	
Rhinocerotid sp.	Rhinocerotid sp.
Moropus sp.	Chalicothere (?) sp.
	Tapirid sp.
Artiodactyla	Artiodactyla
Prosthennops (?) sp.	Platygonus (?) sp.
Ticholeptus sp.	Ticholeptus (?) sp.
Dromomeryx near borealis (Cope)	Dromomeryx near borealis (Cope)
	Blastomeryx (?) sp.
Merycodus cf. nevadensis Merriam	Merycodus sp. a
	Merycodus sp. b
Camelid (?) sp. a	
Camelid (?) sp. b	

Many of the forms recognized in the Sucker Creek fauna are represented likewise in the Skull Spring assemblage by either identical or closely related types. It appears entirely possible that the Sucker Creek faunal stage is a near, if not a direct, chronologic equivalent of that described from Skull Spring, although the deposits in which the former occurs may represent a longer period of accumulation than that recorded by the beds containing the latter horizon. Gazin has pointed out the close resemblance between the Skull Spring fauna and the assemblages known from the Mascall and the Virgin Valley. As in the case of the Skull Spring assemblage, that from Sucker Creek shows a slightly greater resemblance to the Virgin Valley fauna than to the Mascall fauna, and this is especially noticeable in a comparison of the ungulates. Similarity of types is also seen when comparison is made with the fauna from the Pawnee Creek beds of Colorado and with that of the Lower Snake Creek beds of Nebraska.

SYSTEMATIC DESCRIPTION

Carnivora

Canid (?) sp.

Remains of carnivora in the fauna consist chiefly of jaw and limb fragments too incomplete to indicate definite family relationships. One specimen, an $M\underline{1}$, No. 1771, C. I. T. Coll. Vert. Pale. (Plate 1, fig. 4), is complete, however, and may represent a member of the Canidæ, although it appears to be distinct from any known genus of that family. The tooth is semiquadrate in shape with broad heel. It is extremely low-crowned, the cusps barely rising above the general level of the occlusal surface. The paracone and metacone are placed well in from the outer edge, which is marked by a distinct cingulum. A faint anteroposterior ridge runs through the paracone and metacone. A low ridge curves forward and outward around the protocone. A weak protoconule attached to the protocone is likewise connected with the paracone by a faint ridge. The protocone lies entirely in the anterior half of the tooth. A metaconule is present at the postero-external end of the hypocone ridge.

Measurements (*in millimeters*)

Anteroposterior diameter	9.3
Transverse diameter	10.5

Rodentia

Sciurid (?) sp.

A fragmentary ramus without teeth, No. 1779 C. I. T. Coll., suggests a sciurid type, but the determination is by no means certain. Four quadrate cheek-teeth were apparently present as in the Sciuridæ, and the ramus is somewhat heavier and more massive than that in modern representatives of that family.

Chalicomyid sp.

A single tooth fragment, No. 1773 C. I. T. Coll. Vert. Pale. (Plate 1, fig. 2), suggests the presence of a member of the Chalicomyidæ. The specimen unfortunately does not provide a basis for a more definite determination.

Mylagaulus cf. lævis Matthew

A single mylagaulid tooth, No. 1042 C. I. T. Coll. Vert. Pale. (Plate 1, figs. 3, 3a), an upper fourth premolar, is practically identical in size and in structure with specimens from Skull Spring, referred by Gazin[1] to *Mylagaulus* cf. *lævis* Matthew. Five enamel lakes are present on the occlusal surface, although six or seven may have been present originally. The anterior lake has a bifurcate front border and appears to have been formed by the union of two lakes. In the postero-external lake the posterior border is bifurcate and this structure appears also to be the result of a union of two lakes. The external lake is quite small and elliptical in shape, while the others are elongate anteroposteriorly.

A fragment of a right ramus, No. 1774 (Plate 1, fig. 1), bears $M\overline{2}$ and $M\overline{3}$ and the posterior portion of $P\overline{4}$. The posterior molars are simple cylindrical teeth. $M\overline{2}$ possesses four enamel lakes while three lakes are present in $M\overline{3}$.

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[1] C. L. Gazin, *ibid.*, 69–71, 1932.

Measurements of teeth (in millimeters)

	P$\underline{4}$ No. 1042 C.I.T.	M$\overline{2}$ No. 1774 C.I.T.	M$\overline{3}$ No. 1774 C.I.T.
Anteroposterior diameter	8.2	3.8	2.4
Transverse diameter	5.3	3.4	2.4

Proboscidea

Mastodont sp.

Fragments of teeth and incomplete limb elements are recognized as belonging to a mastodont type, but the specimens are not sufficiently complete to permit a more detailed determination.

Perissodactyla

Hypohippus near osborni Gidley

An unworn complete M$\overline{3}$, No. 1769 (plate 2, figs. 4, 4a), and the posterior portion of an upper cheek-tooth, No. 1048 (fig. 2), represent the genus *Hypohippus.* The specimens are so strikingly similar to teeth from the Virgin Valley beds described by Merriam[1] as *Hypohippus* near *osborni,* that Merriam's discussion of the affinities of the Virgin Valley form holds equally well for the Sucker Creek specimens. It may be noted, however, that in No. 1769 a groove running part way down the lingual side of the metaconid is faintly suggested and a tiny tubercle is present at the entrance to the postero-internal valley.

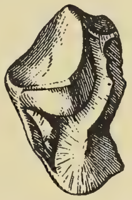

FIG. 2—*Hypohippus* near *osborni* Gidley. Fragment of upper cheek tooth, No. 1048, occlusal view; x1.0. Calif. Inst. Tech. Coll. Sucker Creek, Miocene, Oregon.

Measurements (in millimeters)

M$\overline{3}$, No. 1769, anteroposterior diameter	23.5
M$\overline{3}$, No. 1769, transverse diameter	12.5

Parahippus avus (Marsh)

A number of lower cheek-teeth, Nos. 442 (fig. 3b), 443–445, 1045 (fig. 3a), and 1046 C. I. T. Coll. Vert. Pale., are referred to the species *Parahippus avus* (Marsh) recorded from the Mascall formation of north-central Oregon.[2] The teeth are featured by very strong external cingula and by the presence of cement in the valleys. M$\overline{3}$, No. 1046, possesses a very heavy deposit of cement but has only a weak cingulum. A very low cingular cuspule is present at the base of the external median valley in all of the specimens. The inner walls of the protoconid and hypoconid show a slight crenulation of the enamel and this becomes less distinct with wear. Tiny cuspules may be present at the bases of the interior valleys,

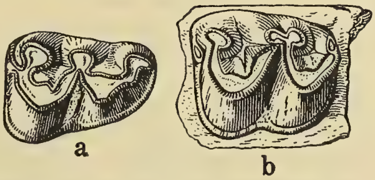

FIG. 3—*Parahippus avus* (Marsh). *a,* P$\overline{2}$, No. 1045, occlusal view; *b,* P$\overline{3}$ or P$\overline{4}$, No. 442, occlusal view; x1.0. Calif. Inst. Tech. Coll. Sucker Creek Miocene, Oregon.

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[1] J. C. Merriam, Univ. Calif. Pub., Bull. Dept. Geol., vol. 6, 257–261, figs. 25–27, 1911.

[2] H. F. Osborn, Mem. Amer. Mus. Nat. Hist., vol. 2, pt. 1, 87, 88, 1918.

attached to the walls of the metaconid and metastylid. The entostylid is a well-developed pillar, rising from the posterior cingulum. Its summit in a little-worn tooth is somewhat lower than that of the entoconid. The metaconid and metastylid are separated by a groove which is distinct for a distance extending approximately half-way to the base of the crown. The metaconid sends a long narrow projection into the antero-interior valley. In one specimen, No. 445, this projection is represented by a separate antero-posteriorly elongated style and there is a prominent buttress on the anterior wall of the protoconid loph. The floors of the interior valleys are situated somewhat above the base of the crown and the valleys are consequently rather shallow in vertical depth, becoming reduced by wear to mere notches. The external valley extends well into the crown throughout all stages of wear.

The Sucker Creek form shows advance over the type found at Skull Spring[1] in greater height of crown, slightly larger size, presence of cement and of a heavy continuous external cingulum. Moreover, the teeth from the Sucker Creek deposits are marked by regular horizontal striations, while in the Skull Spring specimen the surface is irregularly rugose in a vertical direction.

Lower teeth of *P. brevidens* (Marsh) in the collections of the California Institute from the Merychippus zone of the North Coalinga region, California, do not have a strong external cingulum and are of somewhat smaller size. The lower teeth of *P. crenidens* (Scott)[2] are slightly smaller in anteroposterior diameter and the metaconid does not project into the antero-interior valley. In *P. pawniensis* Gidley[3] the metaconid and metastylid are not so distinctly separated as in the Sucker Creek form.

A very close resemblance is seen to exist between the Sucker Creek specimens and a tooth described by Merriam[4] as *Parahippus* cf. *avus* from the Middle Miocene Virgin Valley beds of Nevada.

Only a fragmentary cheek-tooth, No. 1775 (Plate 2, fig. 5), is present of the upper dentition of *Parahippus*. It exhibits no characters to separate it from any of the several species of *Parahippus*.

Measurements of teeth (*in millimeters*)

	Anteroposterior diameter	Greatest transverse diameter (at base)
P$\overline{2}$, No. 1045	19.9	13.0
P$\overline{4}$(?), No. 442	19.5	15.6
M$\overline{1}$(?), No. 443	20.0	14.6
M$\overline{2}$(?), No. 444	19.3	13.1
M$\overline{3}$, No. 1046	21.5	11.6

Merychippus Leidy

Remains of merychippine horses are more numerous than those of the anchitheriine types in the collections from the Sucker Creek beds. The former consist chiefly of isolated upper and lower cheek-teeth, but an incomplete mandible and several limb elements are also present.

F. D. Bode,[5] in a study of a large number of merychippine teeth from the Merychippus zone of the North Coalinga region, found that the majority of the teeth from this horizon exhibit the characters of *Merychippus californicus* Merriam. However, a number of variants were recognized by Bode which approach in their characters those of other described species of *Merychippus*, and in addition one group was established as specifically distinct from all known forms.

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[1] C. L. Gazin, Carnegie Inst. Wash. Pub. No. 418, 77, 78, fig. 10c, 1932.

[2] H. F. Osborn, *op. cit.*, 90–92, fig. 67, 1918.

[3] J. W. Gidley, Bull. Amer. Mus. Nat. Hist., vol. 23, 932, 1907; H. F. Osborn, Mem. Amer. Mus. Nat. Hist., vol. 2, pt. 1, 92–93, 1918.

[4] J. C. Merriam, Univ. Calif. Pub., Bull. Dept. Geol., vol. 6, 261–262, fig. 29, 1911.

[5] F. D. Bode, Carnegie Inst. Wash. Pub. No. 453, art. V, 39–63, 1934.

Similar variation is found among the *Merychippus* teeth in the Sucker Creek collection, although diversity of type is expressed to a lesser extent than in the Coalinga fauna, due in part at least to the much smaller number of specimens available. A majority of the teeth possess the characters of a single species. A second form can also be distinguished and variants are present which approach still other species of *Merychippus*.

Merychippus isonesus (Cope)

The predominating form in the Sucker Creek assemblage exhibits the characters of *Merychippus isonesus*. The upper teeth have curved crowns of moderate length and are heavily cemented. Protocone and hypocone are sub-equal in size and round-oval in shape, with the hypocone slightly more flattened than the protocone. Both protocone and hypocone are discrete cusps during the first stages of wear, with spurs projecting toward protoconule and metaconule, respectively. The hypocone connects with the metaconule at an early stage of wear, while the protocone remains distinct until the tooth is a little more than half-worn. The fossettes are wide and are open at the anterior and posterior ends of the tooth in unworn specimens, but the union of protoconule and metaloph is complete except in P2. The fossettes become completely closed in an early stage of wear. A pli-caballin, pli-protoconule and pli-hypostyle are usually present though not always developed to the same extent in each specimen. The parastyle and mesostyle are prominent, the mesostyle especially so in the premolars.

As the teeth advance in stage of wear, the protocone becomes rounder in cross-section and the prominence of the projecting spur is decreased. The isthmus connecting hypocone and metaconule, at first narrow, becomes almost as wide as the hypocone itself at a stage of wear marked by a union of protocone and protoconule. With increased wear the fossettes become narrower and the enamel plications tend to disappear. In very advanced wear the protocone and hypocone coalesce, converting the post-protoconal valley into a small enamel-enclosed lake.

The teeth from Sucker Creek are shorter-crowned and slightly less curved than teeth of *Merychippus californicus*. Furthermore, the protocone in *M. isonesus* does not usually project quite so far inward beyond the hypocone as is the case in the Coalinga species.

The lower cheek-teeth are moderately long-crowned and heavily cemented. Comparison of the lower cheek-teeth of *M. isonesus* with those of *M. californicus* reveals the following differences: (1) In *M. isonesus* the crowns are shorter and the convexity of the external walls of the protoconid and hypoconid is more pronounced than in *M. californicus;* (2) The anterior horn of the hypoconid loph joins the posterior horn of the protoconid loph at a later stage of wear in *M. isonesus* than in *M. californicus;* (3) In the lower premolars of *M. isonesus* the anterior horn of the hypoconid loph usually joins the posterior horn of the protoconid loph immediately adjacent to the metaconid-metastylid column or it may join directly with the metastylid, producing a very deep external median valley. In *M. californicus*, on the other hand, the union is usually established about half-way between the external and internal sides of the tooth, producing a much shallower external median valley.

The differences noted under (1) appear to be constant, whereas those indicated in (2) and (3) are evidently subject to variation and are not always trustworthy characters of value in distinguishing these two species.

The lower canines in the incomplete mandibular specimen, No. 1059, are small and incisiform and are placed immediately adjacent to I$\overline{3}$. The size of the alveolus for I$\overline{3}$ indicates that this tooth was somewhat larger than the canine.

In the milk teeth of *M. isonesus* from Sucker Creek the protocone and hypocone are conical and the principal axis of the latter cusp runs diagonally across the tooth. As noted by Bode,[1] these characters readily distinguish the milk teeth of *M. isonesus* from those of *M. californicus*. In the latter, the teeth have longer crowns, are well-cemented, and the protocone and hypocone are cylindrical with the principal axis of the hypocone oriented in an anteroposterior direction.

M$\underline{3}$, No. 437 (fig. 4h), is typical of a form whose characters suggest *Merychippus sumani*. The protocone is elongated anteroposteriorly and this cusp remains separate to the base of the crown. The tooth is considerably larger than teeth of average size referred to *M. isonesus*.

Measurements of teeth (in millimeters)

	Antero-posterior diameter	Greatest transverse diameter (exclusive of cement)	Height of crown of unworn specimens
P$\underline{2}$, No. 1049	21.6	15.8	
P$\underline{3}$, No. 1050	19.7	17.2	
P$\underline{4}$, No. 1051	18.9	18.0	
M$\underline{2}$, No. 1053	18.5	17.0	
M$\underline{3}$, No. 1054	17.6	16.3	*a*20.0
M$\underline{3}$, No. 437	21.3	19.0	
P$\overline{2}$, No. 1057	18.4	8.8	
P$\overline{3}$, No. 1057	17.8	10.5	
P$\overline{3}$ or P$\overline{4}$, No. 1052	19.5	*a*10.5	
M$\overline{1}$, No. 1055	18.5	*a*8.5	*a*30.0
M$\overline{2}$, No. 1056	*a*18.1	*a*8.5	*a*30.0
M$\overline{3}$, No. 1058	*a*22.7	*a*7.0	
P$\overline{2}$–M$\overline{3}$, No. 1059	106.4		
Dp$\underline{2}$, No. 441	23.4	14.9	
Dp$\underline{3}$, No. 440	19.7	15.8	
Dp$\underline{4}$(?), No. 439	19.1	16.6	
Dp$\overline{2}$, No. 1047	*a*22.5	12.0	

a, approximate.

Merychippus brevidontus Bode

Three teeth, Nos. 1123, 1124 and 1770, C. I. T. Coll. Vert. Pale. (Plate 2, figs. 1–3a), exhibit the complexity of enamel pattern coupled with shortness of crown which is characteristic of this species as described from the Merychippus zone of California.

In view of the association of this form with a progressive species of *Parahippus* as noted by Bode for the latter horizon, it is well to indicate a similar association in the Sucker Creek fauna.

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[1] F. D. Bode, *op. cit.*, 45, pl. 2, figs. 2 and 3, 1934.

Measurements of teeth (in millimeters)

	$M\underline{2}$ No. 1770 C.I.T.	$M\underline{2}$(?) No. 1123 C.I.T.	$P\overline{2}$ No. 1124 C.I.T.
Anteroposterior diameter	18.5	18.9	20.1
Transverse diameter	17.7	....	11.7

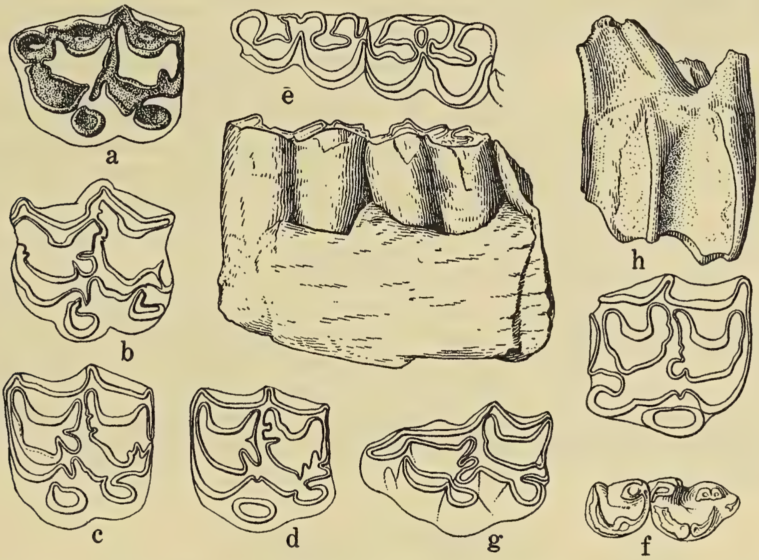

Fig. 4—*Merychippus isonesus* (Cope). *a*, $P\underline{2}$, No. 1049, occlusal view; *b*, $P\underline{3}$, No. 1050, occlusal view; *c*, $P\underline{4}$, No. 1051, occlusal view; *d*, $M\underline{2}$, No. 1053, occlusal view; *e*, $P\overline{2}$ and $P\overline{3}$, No. 1057, lateral and occlusal views; *f*, $M\overline{1}$, No. 1055, occlusal view; *g*, $Dp\underline{2}$, No. 441, occlusal view; *h*, $M\underline{3}$, No. 437, lateral and occlusal views showing type of tooth associated with typical *M. isonesus* and which closely resembles *M. sumani;* x1.0. Calif. Inst. Tech. Coll. Sucker Creek Miocene, Oregon.

Rhinocerotid sp.

Fragments of teeth and of limb elements indicate the presence of a rhinocerotid in the fauna, but a generic determination of the form is not possible on the basis of available material. The fragments suggest a type with relatively long-crowned teeth.

Moropus sp.

Chalicotheres are represented in this collection by a single tooth, a right $M\underline{2}$, No. 1060 C. I. T. Coll. Vert. Pale. (fig. 5), which agrees in character of crown with the description of teeth of *Moropus* given by Holland and Peterson.[1] The tooth is unworn and well preserved. It is semiquadrate in shape with parastyle placed farther forward than the antero-internal corner of the tooth. The ectoloph is sharply inflected, having a W-shape, with prominent parastyle and mesostyle. A faint rib is present on the outer wall

[1] W. J. Holland and O. A. Peterson, Mem. Carnegie Mus., vol. 3, 245–247, 1914.

of the paracone. The outer walls of the paracone and metacone slant inward at an angle of approximately 45 degrees. The crest of the ectoloph is sharp. A small sharp tubercle lies adjacent to the inner wall of the paracone. The protocone is isolated, the protoloph being cut through by the anterior exit of the valley between protocone and paracone. A short sharp crest curves inward and forward from the summit of the protocone. A low sharp crest extending inward from the metacone ends in the hypocone. A deep V-shaped valley extends forward from the posterior end of the tooth between hypocone and metacone. A second exit of the protocone-paracone valley exists between hypocone and protocone. A heavy cingulum is present at the anterior end of the tooth, while a short cingulum extends backward from the protocone. In addition, a posterior cingulum is present and a faint cingulum occurs at the base of the ectoloph. The inner side of the tooth is supported on a large root, elliptical in cross-section, while the parastyle and mesostyle are each supported by a smaller root.

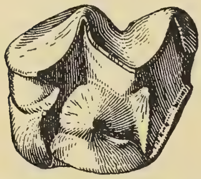

Fig. 5—*Moropus* sp. M$\underline{2}$, No. 1060, occlusal view; x1.0. Calif. Inst. Tech. Coll. Sucker Creek, Miocene, Oregon.

The Sucker Creek specimen is approximately half the size of the corresponding tooth in *Moropus elatus* of the Lower Miocene of Nebraska, the best-known species of that genus.[1] *Moropus merriami* from Virgin Valley apparently approaches *M. elatus* in size, as does also the Skull Spring chalicothere(?). In size, No. 1060 is not far removed from *M. oregonensis* of the John Day region, Oregon. The Sucker Creek form may be determined ultimately as a type specifically distinct from both the Virgin Valley and the Skull Spring forms.

Measurements (in millimeters)

	Moropus, sp. No. 1060 C.I.T.	*M. elatus* No. 2103 Car. Mus.
M$\underline{2}$, anteroposterior diameter	25.4	56.0
M$\underline{2}$, transverse diameter	21.0	41.0

Artiodactyla

Prosthennops(?) sp.

The peccaries are represented by a single M$\overline{3}$, No. 1061 C. I. T. Coll. Vert. Pale. (fig. 6). Four principal cusps are present and are arranged in a rectangle slightly longer antero-posteriorly than transversely. The two anterior cusps are somewhat stouter and stand slightly higher than the posterior pair The heel is about one-third the length of the entire tooth and displays four small cusps, sub-equal in size. A smaller cuspule is present on each side of the last cusp on the heel. The tooth unfortunately presents no characters on which a definite generic determination can be made. It can be readily separated from *Platygonus* by the conical shape of the cusps and an absence of cross-crests. It is distinguished from *Desmathyus* by an absence of a cingulum. In a comparison between third lower molars of *Perchœrus* from the White River and John Day Oligocene and those of *Prosthennops* from the Rattlesnake and Thousand Creek Pliocene, it was observed that the principal cusps in the later genus are stouter and crowd each other, occupying relatively more of the occlusal surface than in the earlier genus. In the earlier form the cusps are distinctly separated by open valleys. In these characters the Sucker Creek specimen approaches *Prosthennops*, but remains intermediate between that genus and *Perchœrus*.

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[1] W. J. Holland and O. A. Peterson, *ibid.*, 222–226, 1914.

The peculiar character of the heel of No. 1061 may or may not have taxonomic importance. The number and size of accessory tubercles on the molars of Recent peccaries have been observed to be highly variable. A type of heel similar to that in No. 1061 is seen in *Perchœrus trichænus* of the John Day and serves to distinguish this species from *P. pristinus* of the same horizon.[1] A specimen of *Prosthennops* in the California Institute collections from the Rattlesnake Pliocene, although notably larger, has an arrangement of cusps on the heel of M$\overline{3}$ very similar to that in the Sucker Creek specimen. *Prosthennops longirostris* Thorpe from the Pliocene of Oregon has also a large number of tubercles on the heel of M.$\overline{3}$

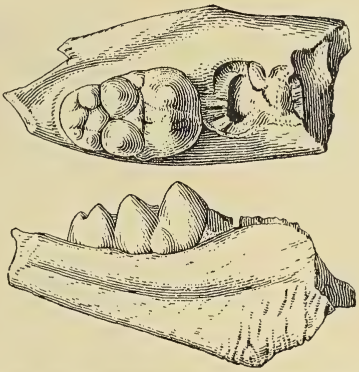

FIG. 6—*Prosthennops* (?) sp. M$\overline{3}$, No. 1061, lateral and occlusal views; x1.0. Calif. Inst. Tech. Coll. Sucker Creek Miocene, Oregon.

Measurements (in millimeters)

Anteroposterior diameter	17.5
Transverse diameter	10.0

Ticholeptus sp.

Oreodont material in the Sucker Creek collection is sufficient to permit generic identification of the form represented, but a definite specific determination is not warranted.

Nos. 1062, 1064 and 1728 (fig. 7) are fragments of jaws bearing upper and lower teeth which, when compared with *Ticholeptus petersoni* Loomis[2] from the Lower Harrison beds of Wyoming, show close agreement in all essential details of tooth pattern but differ slightly in size. The lower jaw fragments are slightly larger than *T. petersoni*, but the upper teeth in No. 1728 are slightly smaller than the comparable teeth in that species. Also, in No. 1728, M$\underline{1}$ and M$\underline{2}$ have small median inner cuspules, M$\underline{3}$ a prominent cuspule and in addition a smaller cuspule at the base of the posterior inner crescent. These tubercles do not appear on the molars of the specimen of *T. petersoni* available for comparison. However, sufficient similarity is evident on which a reference of the Sucker Creek form to the genus *Ticholeptus* may be made.

[1] H. S. Pearson, Bull. Amer. Mus. Nat. Hist., vol. 48, 95, 1923.

[2] F. B. Loomis, Amer. Jour. Sci., ser. 5, vol. 6, 222–228, 1923.

The two oreodont teeth from Skull Spring, referred by Gazin[1] to *Ticholeptus*(?) sp., show considerable resemblance in size and in pattern to corresponding teeth of *T. petersoni* and would appear to be in fact indistinguishable from that species.

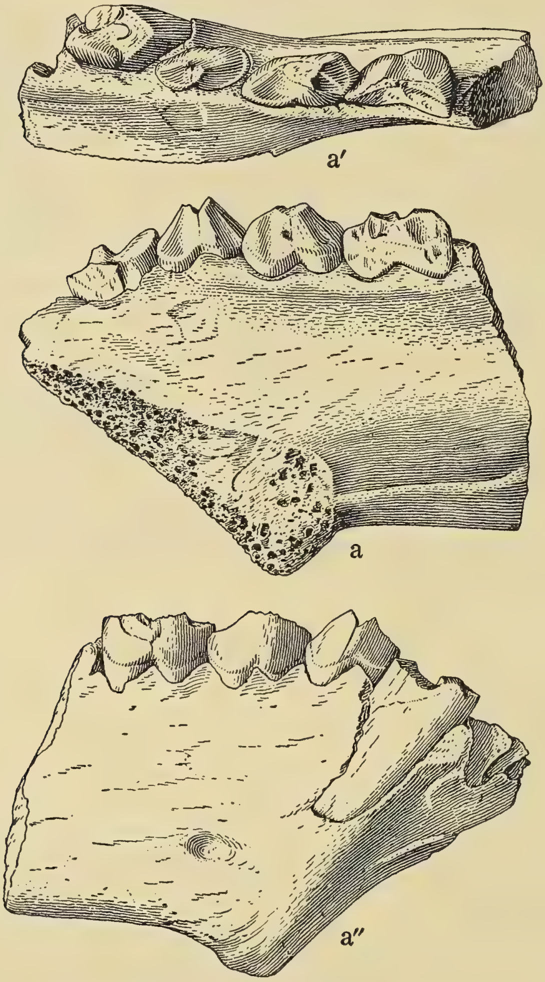

Fig. 7—*Ticholeptus* sp. *a*, Fragment of right ramus with $P\overline{1}$–$P\overline{4}$, No. 1062, lateral and occlusal views; x1.0. Calif. Inst. Tech. Coll. Sucker Creek Miocene, Oregon.

It is interesting to note furthermore that a specimen in the collections of the California Institute from the Mascall Miocene of the John Day basin demonstrates for the first time the presence of *Ticholeptus* in that horizon. In this specimen, No. 1730 (fig. 8), a lower jaw fragment with $P\overline{4}$ and $M\overline{1}$, the anterior crest is bifurcate, a feature which Loomis[2] regards as characteristic of *Ticholeptus* and *Metoreodon*. However, the pillar-like cusp on the median crest is not enlarged and does not extend so far forward as in *Metoreodon*, nor is the posterior portion of the tooth reduced as in that genus. No. 1730 is slightly smaller than the corresponding part in *T. petersoni* and the pillar-like cusp on the median crest is not so enlarged. Close resemblance to the Mascall specimen in this respect and in size is exhibited by a lower fourth premolar, No. 389, from Skull Spring. Nos. 389 and 1730 may belong to a species distinct from that represented by Nos. 387, 388, from Skull Spring.

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[1] C. L. Gazin, Carnegie Inst. Wash. Pub. No. 418, pp. 81–82, figs. 15, a and b, 1932.

[2] F. B. Loomis, Bull. Amer. Mus. Nat. Hist., vol. 51, 12, 1924.

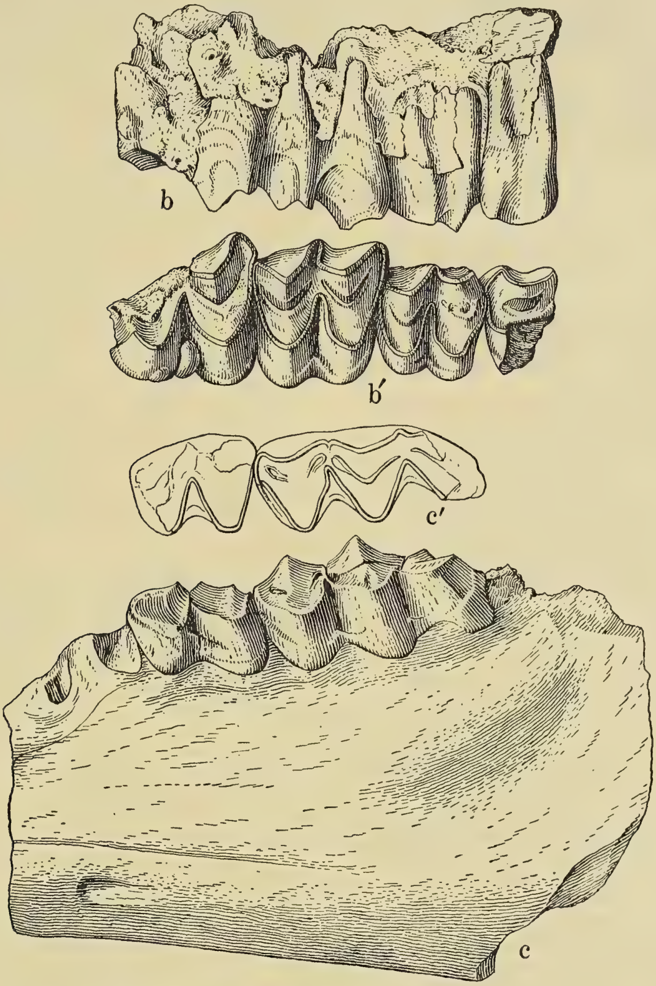

Fig. 7—*Ticholeptus* sp. *b*, Fragment of right maxillary with P$\underline{4}$–M$\underline{3}$, No. 1728, lateral and occlusal views; *c*, fragment of left ramus with M$\overline{2}$ and M$\overline{3}$, No. 1064, lateral and occlusal views; x1.0. Calif Inst. Tech. Coll. Sucker Creek Miocene, Oregon.

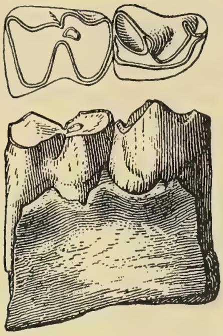

FIG. 8—*Ticholeptus* sp. P$\overline{4}$ and M$\overline{1}$, No. 1730, lateral and occlusal views; x1.0. Calif. Inst. Tech. Coll. Mascall Miocene, Oregon.

Measurements (*in millimeters*)

No. 1062:	
Anteroposterior diameter, P$\overline{1}$–P$\overline{4}$	50.1
Anteroposterior diameter, P$\overline{2}$–P$\overline{4}$	39.0
No. 1064:	
Anteroposterior diameter, M$\overline{2}$–M$\overline{3}$	46.6
Transverse diameter, M$\overline{2}$	11.6
Transverse diameter, M$\overline{3}$	11.9
No. 1728:	
Anteroposterior diameter, P$\underline{4}$–M$\underline{3}$	*a*61.
Anteroposterior diameter, P$\underline{4}$	10.1
Anteroposterior diameter, M$\underline{1}$	*a*14.7
Anteroposterior diameter, M$\underline{2}$	17.8
Anteroposterior diameter, M$\underline{3}$	*a*23.4
Transverse diameter, P$\underline{4}$	*a*12.8
Transverse diameter, M$\underline{1}$	13.7
Transverse diameter, M$\underline{2}$	15.1
Transverse diameter, M$\underline{3}$	*a*16.2
No. 1730:	
Anteroposterior diameter, P$\overline{4}$	12.8
Transverse diameter, P$\overline{4}$	9.6
Anteroposterior diameter, M$\overline{1}$	13.0
Transverse diameter, M$\overline{1}$	9.1
No. 1527 C. I. T. Coll. Vert. Pale., *T. petersoni:*	
Anteroposterior diameter, P$\overline{2}$–P$\overline{4}$	34.5
Anteroposterior diameter, M$\overline{2}$–M$\overline{3}$	42.3
Transverse diameter, M$\underline{2}$	11.2
Transverse diameter, M$\underline{3}$	11.7
Anteroposterior diameter, P$\underline{4}$–M$\underline{3}$	64.0
Anteroposterior diameter, P$\underline{4}$	10.9
Anteroposterior diameter, M$\underline{1}$	15.5
Anteroposterior diameter, M$\underline{2}$	19.7
Anteroposterior diameter, M$\underline{3}$	23.0
Transverse diameter, P$\underline{4}$	13.0
Transverse diameter, M$\underline{1}$	16.4
Transverse diameter, M$\underline{2}$	17.3
Transverse diameter, M$\underline{3}$	18.3

Merychyus (?) sp.

A single tooth, No. 1063 (Plate 1, figs. 7, 7a), may belong to the genus *Merychyus.* The anterior crest is simple and a pillar-like cusp projects forward slightly at the point of union of the median crest with the posterior crescent. The posterior basin is completely enclosed and a posterior intermediate crest is suggested. This specimen resembles P$\overline{4}$ of *Merychyus,* as illustrated by Loomis.[1]

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[1] F. B. Loomis, *op. cit.*, 13, fig. 7, 1924.

Measurements (in millimeters)

Anteroposterior diameter	12.9
Transverse diameter	8.4

Dromomeryx near borealis (Cope)

A species of *Dromomeryx* close to or identical with *Dromomeryx borealis* (Cope) is represented by a number of isolated teeth and a few limb elements. Unfortunately, specimens of horn-cores, on which the description of the species is partially based, are not present.

$P\underline{2}$, $P\underline{4}$ and $M\underline{2}$, Nos. 1066, 1067 and 1068, C. I. T. Coll. Vert. Pale. (figs. 9a, b, c), appear to be indistinguishable from corresponding teeth in Cope's type specimens. They likewise appear to be specifically inseparable from corresponding teeth of No. 1542, Carnegie Mus. Coll., from the Upper Miocene of Montana, assigned by Douglass to *D. borealis*.[1] However, a comparison of the lower molars from Sucker Creek with illustrations given by Douglass of the lower dentition of *D. borealis* reveals some differences which may be significant.

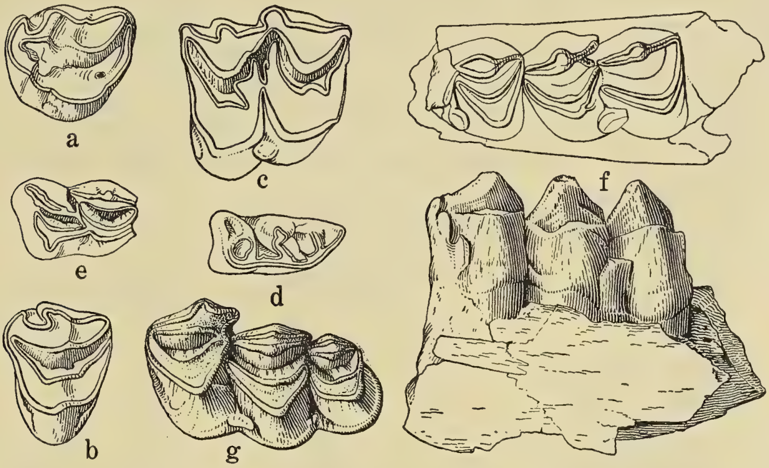

FIG. 9—*Dromomeryx* near *borealis* (Cope). *a*, $P\underline{2}$, No. 1066, occlusal view; *b*, $P\underline{4}$, No. 1067, occlusal view; *c*, $M\underline{2}$, No. 1068, occlusal view; *d*, $P\overline{3}$, No. 1069, occlusal view; *e*, $P\overline{4}$, No. 1729, occlusal view; *f*, $M\overline{2}$ and portion of $M\overline{1}$, No. 1071, lateral and occlusal views; *g*, $M\overline{3}$, No. 1072, occlusal view; x1.0. Calif. Inst. Tech. Coll. Sucker Creek Miocene, Oregon.

In the Sucker Creek specimens the antero-external crescent, after moderate wear, unites with the postero-internal crescent. A small enamel process is also present, extending postero-externally from a point near the posterior end of the antero-internal crescent to the point of union of the antero-external and postero-internal crescents.

The illustration of the lower teeth of *D. borealis* given by Douglass, shows the union of antero-external and postero-internal crescents occurring in the much-worn $M\overline{1}$ but not in $M\overline{2}$ and $M\overline{3}$. Moreover, there appears to be no trace of the small enamel process described above. $M\overline{3}$ of the Montana form, in fact, shows the most marked difference from the comparable tooth in the Sucker Creek species. In the former, a strong union takes place between the anterior ends of the internal and external crescents of the second lobe. Furthermore, the posterior lobe in No. 1072 from Sucker Creek (fig. 9g) appears to be rotated inward and away from the second lobe more than in the Montana specimen.

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[1] E. Douglass, Ann. Carnegie Mus., vol. 5, plate 63, figs. 1 and 3, 1909.

The lower teeth of *D. borealis* illustrated by Douglass are those of No. 827 Carnegie Mus. Coll. The upper dentition associated with this series is also figured. The upper teeth of No. 827 differ principally from those in another specimen, No. 1542 Carnegie Mus. Coll., in absence of accessory spurs on the wings of the internal crescents of the molars. Douglass assigned both No. 827 and No. 1542 to the species *D. borealis*, because of similarities noted in the characters of skull and horn in these types.

It is possible that the lower teeth associated with the type of upper dentition present in No. 1542 and in Cope's specimens resembled more closely the Sucker Creek material than does No. 827. If the dental characters have a specific importance equal to or greater than that of the horns, the Sucker Creek form and No. 1542 from Montana may be referred to *D. borealis*. On the other hand, No. 827 from Montana should be regarded as belonging to a distinct species. On this basis also, the material from Skull Spring and that described by Sinclair[1] from the Snake Creek beds should be referred to *D. borealis*. In the absence of skull or horn material it does not appear desirable, however, to definitely identify the Sucker Creek form as of the species *D. borealis*.

Measurements (in millimeters)

	Anteroposterior diameter	Transverse diameter
P$\underline{2}$, No. 1066	16.3	14.6
P$\underline{4}$, No. 1067	14.0	17.2
M$\underline{2}$, No. 1068	22.2	20.5
P$\overline{3}$, No. 1069	16.6	7.6
M$\overline{1}$(?), No. 1070	*a*20.5	13.0
M$\overline{2}$, No. 1071	21.8	13.5
M$\overline{3}$, No. 1072	......	13.5

a, approximate.

Merycodus cf. nevadensis Merriam

Merycodont remains consist of a fragmentary horn, No. 1073 C. I. T. Coll. Vert. Pale. (fig. 10), and two lower jaw fragments, No. 1074, bearing an M$\overline{2}$, and No. 1772, bearing an M$\overline{3}$ (Plate 1, figs. 5–6b). These specimens indicate a rather small form of *Merycodus*, possibly close to *M. nevadensis* Merriam,[2] from the Virgin Valley beds of Nevada.

The anterior tine of the horn and the base of the beam are missing in No. 1073. Judging from the depth of the nutrient canals, this specimen represents a fully adult individual. It is decidedly more slender than specimens in the large series of horns of *Merycodus loxocerus* Furlong,[3] representing individuals in various stages of growth from the Upper Miocene of Nevada. In *M. loxocerus* the beam, relative to the length of the tines, is considerably elongated and individual horns may be more slender than those of *M. furcatus*.

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[1] W. J. Sinclair, Proc. Amer. Philos. Soc., vol. 54, 94–95, 1915.

[2] J. C. Merriam, Univ. Calif. Pub., Bull. Dept. Geol., vol. 6, 284–285, 1911.

[3] E. L. Furlong, Carnegie Inst. Wash. Pub. No. 453, 1–10, 1934.

The beam is slightly convex toward the front. Cross-sections of the beam are shown in figure 10.

The teeth represent young adult individuals and resemble closely in size comparable teeth in *M. loxocerus, M. nevadensis* and in a species of *Merycodus* recorded from Skull Spring.[1] The anterior crests are flanked by prominent styles at each end. The posterior crest of M$\overline{2}$ possesses also a strong posterior style. Both crests have strong median ribs on their lingual surfaces. The crescents are not so harply ridged as in *M. loxocerus* and have a rounded appearance. A median cuspule is present between the outer crescents of M$\overline{2}$. It is not shown in M$\overline{3}$, but the crown of this tooth has not fully emerged. M$\overline{2}$ has no trace of a vertical fold on the anterior face, but a suggestion of a fold is seen in M$\overline{3}$. In size of teeth, smallness of third lobe in M$\overline{3}$, and in slenderness of horn, the Sucker Creek form resembles *Merycodus nevadensis* more closely than it does any other known merycodont species. The present species may be identical with that from Skull Spring which it resembles in size and in prominence of styles on the inner crests of the lower molars. In latter character as well as in the more rounded crescents and in slenderness of horn, it differs from *M. loxocerus*. It is smaller than *M. furcatus, M. necatus* and *M. osborni.*

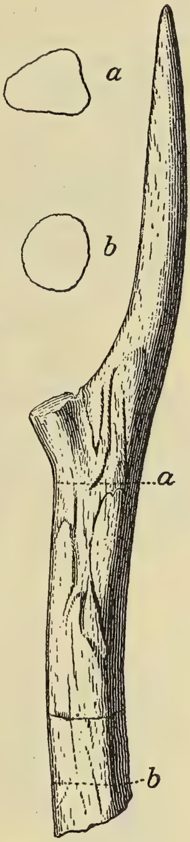

Fig. 10—*Merycodus* cf. *nevadensis* Merriam. Fragment of left horn-core, No. 1073, outer view; *a* and *b*, cross-sections; x1.0. Calif. Inst. Tech. Coll. Sucker Creek Miocene, Oregon.

Measurements (in millimeters)

Length of tine above bifurcation	50.1
Length of beam below bifurcation (incomplete)	58.5
M$\overline{2}$, anteroposterior diameter	8.3
M$\overline{2}$, greatest transverse diameter	4.6
M$\overline{3}$, anteroposterior diameter at alveolar border	10.5
M$\overline{3}$, greatest transverse diameter	4.7

Camelid (?) sp. a

A lower jaw fragment, No. 1065 (fig. 11), with M$\overline{1}$ and partially emerged M$\overline{2}$, resembles the corresponding part of a lower jaw of *Paratylopus cameloides* (Wortman) from the Upper John Day, but differs in somewhat larger size and in slightly greater hypsodonty. No. 1065 compares favorably in size with *Miolabis transmontanus* (Cope) and may belong to a form closely related to this species.

The teeth have prominent median and posterior pillars on their lingual surfaces. The antero-internal corner of M$\overline{1}$ is missing and the same portion of M$\overline{2}$ is not sufficiently exposed to show whether or not anterior pillars were present. M$\overline{1}$ has a median outer cuspule. The base of M$\overline{2}$ is not visible. M$\overline{1}$ has an anterior cingulum from the lingual end of which a slight vertical enamel fold is developed. An incipient development of this feature is seen in M$\overline{2}$.

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[1] C. L. Gazin, Carnegie Inst. Wash. Pub. No. 418, 85, 1932.

Measurements (in millimeters)

M$\overline{1}$, anteroposterior diameter	14.5
M$\overline{1}$, transverse diameter	9.1
M$\overline{2}$, anteroposterior diameter	17.2
M$\overline{2}$, transverse diameter	9.0
Depth of jaw below M$\overline{2}$	*a*26.9

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a, approximate.

Camelid (?) sp. b

A number of foot and limb elements, including an unciform co-ossified with a portion of the vestigial fifth digit, a patella and a pisiform, suggest a camelid larger than that previously recorded. These specimens may show some resemblance in size to *Alticamelus* or *Megatylopus*.

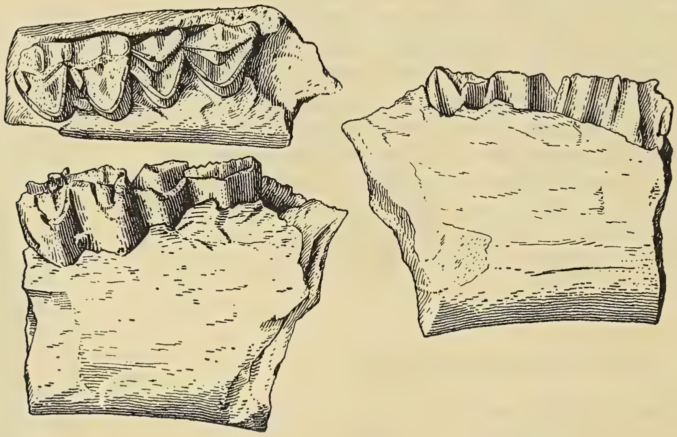
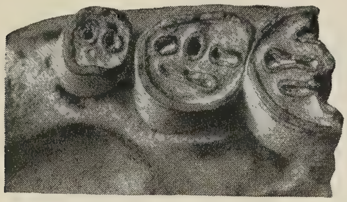


FIG. 11—*Camelid* (?) sp. a. M$\overline{1}$ and M$\overline{2}$, No. 1065, lateral and occlusal views; x1.0. Calif. Inst. Tech. Coll. Sucker Creek Miocene, Oregon.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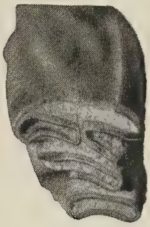
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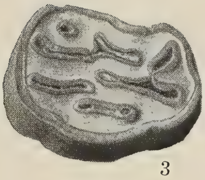
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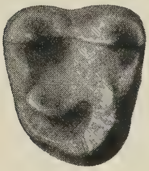
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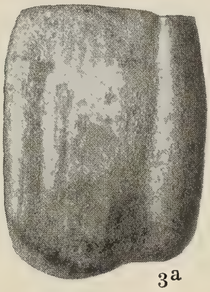
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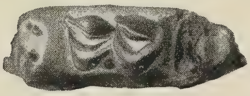
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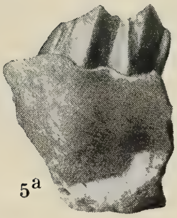
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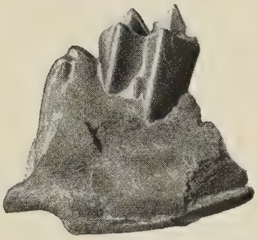
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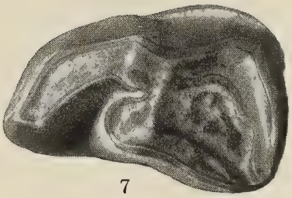
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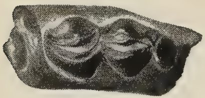
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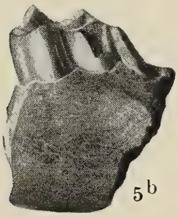
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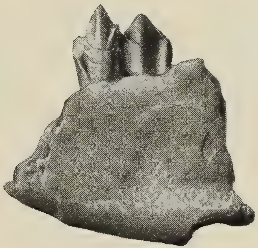
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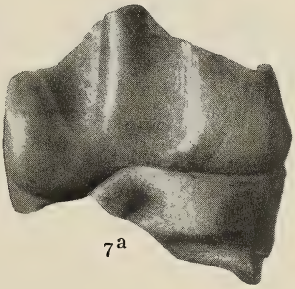
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Mylagaulus cf. *lævis* Matthew

FIG. 1—Fragment of right ramus bearing M$\overline{2}$, M$\overline{3}$ and portion of P$\overline{4}$, No. 1774, occlusal view; x4.
FIGS. 3, 3*a*—P$\underline{4}$, No. 1042, occlusal and inner views; x3.

Chalicomyid sp.

FIG. 2—Upper cheek tooth, No. 1773, occlusal view; x4.

Canid (?) sp.

FIG. 4—M$\underline{1}$, No. 1771, occlusal view; x2.

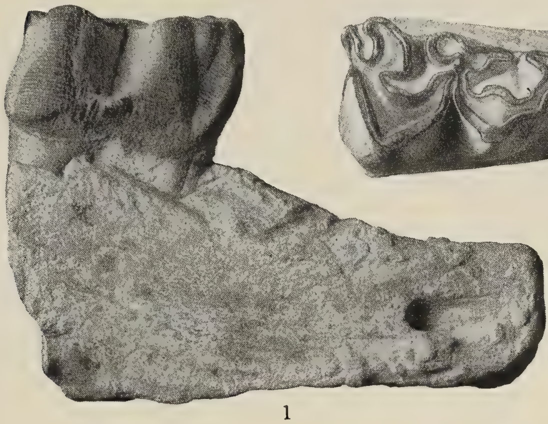
Merycodus cf. *nevadensis* Merriam

FIGS. 5, 5*a*, 5*b*—M$\overline{3}$, No. 1772, lateral and occlusal views; x1.5.
FIGS. 6, 6*a*, 6*b*—M$\overline{2}$, No. 1074, lateral and occlusal views; x1.5.

Merychyus (?) sp.

FIGS. 7, 7*a*—P$\overline{4}$, No. 1063, lateral and occlusal views; x3.

Calif. Inst. Tech. Coll. Sucker Creek Miocene, Oregon.



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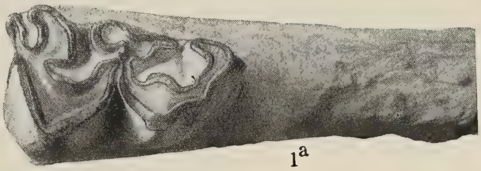

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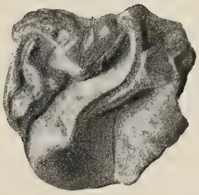

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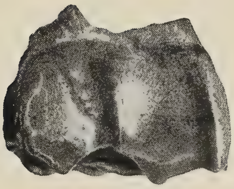

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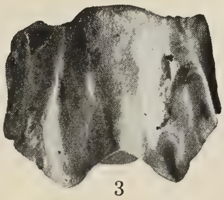

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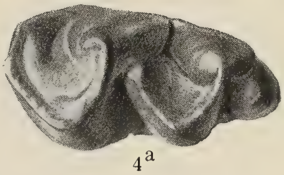

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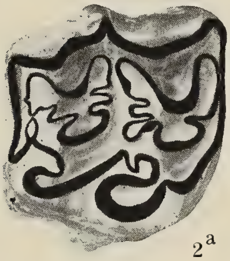

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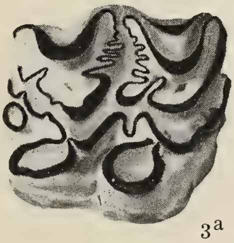

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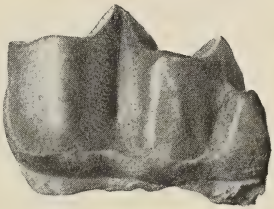

4

Merychippus brevidontus Bode

Figs. 1, 1*a*—P$\overline{2}$, No. 1124, lateral and occlusal views; x1.5.
Figs. 2, 2*a*—M$\underline{2}$, No. 1770, lateral and occlusal views; x1.5.
Figs. 3, 3*a*—M$\underline{2}$(?), No. 1123, lateral and occlusal views; x1.5.

Hypohippus near *osborni* Gidley

Figs. 4, 4*a*—M$\overline{3}$, No. 1769, lateral and occlusal views; x1.5.

Parahippus sp.

Fig. 5—Upper cheek tooth, No. 1775, occlusal view; x1.5.

Calif. Inst. Tech. Coll. Sucker Creek Miocene, Oregon.

CONTRIBUTIONS TO PALÆONTOLOGY

VIII

ARTIODACTYLA FROM THE SESPE OF THE LAS POSAS HILLS, CALIFORNIA

By Chester Stock

With one plate

[Issued July 20, 1935]

ARTIODACTYLA FROM THE SESPE OF THE LAS POSAS HILLS, CALIFORNIA

INTRODUCTION

The artiodactyla found at the Kew Quarry site in the Sespe deposits of the Las Posas Hills, Ventura County, California, comprise at present three forms, namely a camelid, the genus *Hypertragulus*, and possibly a bothriodont. This assemblage is again noteworthy in furnishing information of value in establishing the relationships of the Kew Quarry fauna to the John Day and White River faunal stages. At least one of these recorded forms from the Upper Oligocene extends considerably the known geographic distribution in North America of the particular group to which it belongs.

Dyseotylopus migrans n. gen. and n. sp.

Type specimen—No. 1721 Calif. Inst. Tech. Vert. Pale. Coll., a crushed skull (Plate 1, figure 1).

Diagnostic characters—Larger than known species of *Pœbrotherium*, but similar to this genus in slenderness of skull. Maxillary fossa broad. Molars compressed transversely and higher crowned than in *Pœbrotherium* or in *Paratylopus*. Outer walls of molars flatter and styles distinctly less prominent than in these genera. Mesostyle present, but does not extend full depth of crown.

Description—The type specimen of this genus is represented by a crushed skull which lacks among other parts the anterior end of the snout bearing the canines and incisors. No. 1721 evidently resembles in slenderness of skull and in size the larger species of *Pœbrotherium*. Unfortunately, because of the crushed condition, it is not always possible to determine beyond all doubt some of the major diagnostic characters, but there still remains a high degree of probability in the interpretation of the structural features as they are now revealed.

However, it is difficult to demonstrate with any degree of certainty whether the orbits were closed or open in back. Judging from the fragments which remain on the right side, the orbit may have been open as in *Pœbrotherium*, but if this is really the case the frontal process was carried downward to a considerable extent.

The wall of the face anterior to the orbit is brecciated, but the extent to which the bone fragments extend upward, toward the nasal border, makes it appear reasonably certain that the structure of the skull in this region was like that in *Pœbrotherium*. In other words, a pre-orbital vacuity may have been present, but its size may not have been as large as that of the vacuity in *Pseudolabis*. A maxillary fossa of relatively large size is clearly outlined. In this respect resemblance to *Pseudolabis* and to specimens of *Pœbrotherium* is apparent. Extent of this fossa is greater than that generally seen in skulls of the latter genus. No marked depression is evident along the median line at the anterior ends of the frontals as in the skull of *Pseudolabis dakotensis*.

Compared with the type of *Pœbrotherium andersoni* (No. 17358 Amer. Mus. Nat. Hist.) the cranial region of the skull in the Sespe species corresponds in length to the former, but the facial region is distinctly longer. The skull in No. 1721 may have been as long as that of *Paratylopus sternbergi*, but it is comparatively more slender for its size. The orbit is smaller in our specimen and the large facial fossa noted in No. 1721 is lacking in the John Day type.

In so far as the structures can be determined, considerable similarity prevails between the Sespe species and *Pœbrotherium* in the posterior region of the skull adjacent to the external auditory meatus. Only the upper rim of this opening is preserved and the bulla is crushed and in large part broken away. The paroccipital process resembles that in *Pœbrotherium*, with the plate in front somewhat broader anteroposteriorly. Evidently a deep pit, like that in *Pœbrotherium*, was present between this process and the occipital condyle. Moreover, the condyles do not project backward beyond the level of the occiput, but have a position similar to that in the latter genus. A deep depression is present on either side of the base of the occiput above the condyles.

The lateral compression of the teeth is due in part to the crushing to which the specimen has been subjected. However, with allowance made for this crushing, the teeth in No. 1721 are relatively narrower for their length than those in *Pœbrotherium* or in *Paratylopus*. The teeth are likewise longer-crowned.

P$\underline{1}$ was two-rooted, in which respect the Sespe form agrees with *Pœbrotherium* and differs apparently from *Pseudolabis*. Matthew states that P$\underline{1}$ is caniniform in *P. dakotensis*. The diastema between P$\underline{1}$ and P$\underline{2}$ measures approximately 12 mm. in the Sespe specimen. This length is greater than in *Pœbrotherium* but, relative to length of tooth-row, perhaps no more so than in *Pseudolabis*. Only the base of the crown of P$\underline{4}$ is preserved on the right side of the skull; on the left the crown of this tooth is crushed and the enamel wall on the inner side is split. However, the type of crown present in No. 1721 would appear to resemble that in *Pœbrotherium* and to differ to this extent from that in *Pseudolabis*. The median rib of the outer face is more reduced than in the latter genera.

The molar teeth in the Sespe specimen form a longer series, the individual teeth being larger, narrower, and of a distinctly more slender appearance than in *Paratylopus sternbergi*. Furthermore, the external walls are noticeably flatter and the styles distinctly less prominent than in the latter. The compression of the teeth and the flattening of the outer walls present features that are more accentuated in *Dyseotylopus* than in *Pseudolabis*.

M$\underline{1}$ possesses a mesostyle and this is more prominently developed than in the comparable tooth of *Pseudolabis*. It is present also in M$\underline{2}$, but does not continue downward on the tooth crown to the occlusal margin.

Relationships—Dyseotylopus is evidently an advanced pœbrothere, larger and with longer-crowned, narrower cheek-teeth than in typical *Pœbrotherium* of the White River. The Sespe type is clearly distinct from *Paratylopus*. *Dyseotylopus* is not so robust as *Pseudolabis*, and in the former the reduction in size of styles and the flattening of the external walls of the upper teeth are carried even farther than similar features seen in the latter type.

It is unfortunate that, in absence of the skull, no direct comparisons can be made with the genotype of *Protomeryx*. Matthew[1] has reviewed the status of this genus and has indicated that the type, *Protomeryx halli*, described by Leidy, came from deposits which can be regarded as the equivalent of the Leptauchenia and Protoceras beds. Matthew described a second species, *Protomeryx campester*, from the Leptauchenia zone of northeastern Colorado. With reference to possible relationship of *Dyseotylopus* to *Protomeryx*, it is significant to note in Matthew's description and illustration that *P. campester* possessed a large diastema behind P$\overline{1}$ and that the teeth are higher-crowned and more compressed than in *Paratylopus sternbergi*. Possibly *Dyseotylopus* and *Protomeryx* are congeneric.

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[1] W. D. Matthew, Mem. Amer. Mus. Nat. Hist., vol. 1, pt. 7, 422–423, fig. 29, 1901.

Apparently the species name *cedrensis* was also applied to this type by Matthew, for this name appears in the faunal list (*vide supra*, p. 358) and in the legend below the text-figure (p. 422, fig. 29) illustrating the type specimen of *Protomeryx campester*. Although the name *cedrensis* appears first in the text and also accompanies the figure of the type specimen of *P. campester*, it is evident that Dr. Matthew decided to use the name *campester* instead. *P. cedrensis* and *P. campester* are therefore synonymous and should not be regarded as separate species.

Comparative measurements (in millimeters) of superior dentition

	Dyseotylopus migrans No. 1721 C.I.T.	Pseudolabis dakotensis No. 9807 A.M.N.H.	Pœbrotherium labiatum No. 6520 A.M.N.H.	Pœbrotherium andersoni No. 17358 A.M.N.H.	Pœbrotherium eximium No. 632 A.M.N.H.
Length from anterior end of P$\underline{1}$ to posterior end of M$\underline{3}$........	*a*97.1	107.5	....	71.6	73.0
Length from anterior end of P$\underline{2}$ to posterior end of M$\underline{3}$........	*a*78.1	84.6	64.1	58.3	64.4
P$\underline{4}$, anteroposterior diameter....	10.0	11.4	7.8	8.1	9.0
M$\underline{1}$, anteroposterior diameter....	15.0	*a*15.3	11.1	10.0	10.7
M$\underline{2}$, anteroposterior diameter....	19.7	18.2	13.6	11.7	13.7
M$\underline{3}$, anteroposterior diameter....	20.6	19.7	14.3	12.7	13.8

a, approximate.

Hypertragulus fontanus n. sp.

Type specimen—A crushed skull with cheek-tooth series P$\underline{2}$-M$\underline{3}$ and with a portion of P$\underline{1}$ on the right side, No. 473 Calif. Inst. Tech. Vert. Pale. Coll. (Plate 1, fig. 3).

Referred specimen—Fragment of right ramus of mandible with P$\overline{1}$–M$\overline{3}$, No. 1723 C. I. T. (Plate 1, figs. 4, 4*a*).

Specific characters—In size more like *Hypertragulus calcaratus* from the White River than like *H. hesperius* from the John Day. Distinguished principally by absence of cingula in posterior upper molars and by narrowness of shelf between walls of inner crescents in these teeth. Upper premolar series, P$\underline{2}$-P$\underline{4}$, shorter in relation to length of molar series than in *H. calcaratus*.

Description—The type specimen of this species represents a fully adult individual resembling in size individuals of *H. calcaratus*. The John Day Hypertragulidæ, represented by *H. hesperius* and by *Allomeryx planiceps*, are generally larger and more progressive in this character than the earlier Oligocene forms from the White River. However, variation in this feature is evident among the John Day members of the group. Lull[1] has described *Hypertragulus minutus* from the Upper John Day, and the individual on which this species is based is actually smaller than the type from the Las Posas Hills Sespe.

M$\underline{2}$ and M$\underline{3}$ exhibit no cingula on the anterior and posterior sides of the crowns and the incipient mesostyle, seen in molars of *H. calcaratus*, is likewise absent. Moreover, the shelf forming the floor of the valley between the inner crescents is narrower anteroposteriorly than in the latter species. P$\underline{2}$ and P$\underline{3}$ are small. The diastema between P$\underline{1}$ and P$\underline{2}$ appears to be comparable in length to that observed in *H. calcaratus*.

A lower jaw fragment with teeth, referred to *Hypertragulus fontanus*, is shown in Plate 1, figures 4, 4*a*.

The Sespe species from the Kew Quarry locality comprises individuals of smaller size than those represented by specimens from the Tecuya beds of southern California. In the latter[2] the upper molars are without cingula in

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[1] R. S. Lull, Amer. Jour. Sci., ser. 5, vol. 4, 115, 1922.

[2] C. Stock, Univ. Calif. Publ. Bull. Dept. Geol., vol. 12, 269–270, figs. 2 and 3, 1920.

No. 23603 Univ. Calif. Coll., but an anterior cingulum is present in the molars of No. 23598 Univ. Calif. Coll.

Measurements (in millimeters)

	Hypertragulus fontanus n. sp. Type No. 473 C. I. T.
Length of series, P$\underline{2}$–M$\underline{3}$	24.9
M$\underline{3}$, greatest length, measured parallel to outer side	6.9
M$\underline{3}$, greatest width normal to outer side	6.4

	Hypertragulus fontanus n. sp. No. 1723 C. I. T.
Length of series, P$\overline{3}$–M$\overline{3}$	24.8
Length of diastema in front of P$\overline{2}$ (approximate)	5.2
Length of diastema behind P$\overline{2}$	2.3
Depth of ramus below middle of P$\overline{3}$	5.9

(?)Bothriodon cf. brachyrhynchus (Osborn and Wortman)

The possibility of an anthracothere in the fauna is indicated at present by a single fragmentary specimen. No. 1722 Calif. Inst. Tech. Vert. Paleo. Coll. (Plate 1, fig. 2) consists of a portion of the maxillary with Dp$\underline{3}$ and Dp$\underline{4}$. The crown of Dp$\underline{3}$ is not perfectly preserved, while that of Dp$\underline{4}$ is practically complete. Comparison has been made particularly with No. 579 in the collections of the American Museum of Natural History, a specimen collected in the Upper Oreodon beds of the White River group, South Dakota. Through the courtesy of Dr. F. B. Loomis a milk dentition of *Agriochœrus antiquus* has also been available.

Dp$\underline{4}$ in No. 1722 from the Sespe is narrower, relative to its anteroposterior diameter, than the comparable tooth in *B. brachyrhynchus.* Moreover, the parastyle is more strongly developed, while the mesostyle is weaker in our specimen than in No. 579. The anterior intermediate cusp is distinct and well developed. This tooth differs from Dp$\underline{4}$ in *Agriochœrus* in presence of intermediate cusp, more strongly developed anterior and posterior cingula, wider median valley, and stronger parastyle. There still remains, however, considerable resemblance between these teeth.

Unfortunately, only the posterior portion of Dp$\underline{3}$ remains. In this, however, the size of the posterointernal cusp is like that in the anthracotheres. It likewise differs in shape and in position from the comparable cusp in *Agriochœrus.* In the latter, the cusp has a more forward position with reference to the posteroexternal cusp than in the Sespe specimen.

Several genera and species of anthracotheres have been described from the Oligocene of North America, and it is by no means certain that the Sespe form belongs to the genus *Bothriodon* (*Ancodon*). Presence of this type in the Kew Quarry fauna is significant, particularly if it proves to be an anthracothere, since it emphasizes again the difference between the fauna from the Sespe of the Las Posas Hills and that from the John Day of eastern Oregon. These mammals remain unrecorded in the faunal assemblages from the John Day, but they can not be regarded as restricted in their vertical range to the Oligocene, since they are known to occur in the Lower Miocene (Lower Rosebud) of the western Great Plains.

Measurements (in millimeters)

	No. 1722 C.I.T.	No. 579 A.M.N.H.
Dp$\underline{4}$, greatest anteroposterior diameter measured along outer side	17.4	17.3
Dp$\underline{4}$, greatest transverse diameter across paracone and protocone	15.4	16.4

SUMMARY

Three artiodactyls are recorded from the Kew Quarry site (Locality 126 Calif. Inst. Tech. Vert. Pale.) of the Sespe deposits in the Las Posas Hills, Ventura County, California. These comprise a new genus and species of camel, *Dyseotylopus migrans,* a new species of *Hypertragulus, H. fontanus,* and possibly an anthracothere.

Dyseotylopus is more advanced than *Pœbrotherium* and differs in its structural characters from *Paratylopus* and *Pseudolabis.* The Sespe form is possibly congeneric with *Protomeryx.* In view of the close resemblance between certain mammals occurring in the Kew Quarry fauna and comparable species in the John Day, this difference between the camels from the two horizons furnishes a striking exception.

PLATE 1

Dyseotylopus migrans n. gen. and n. sp.

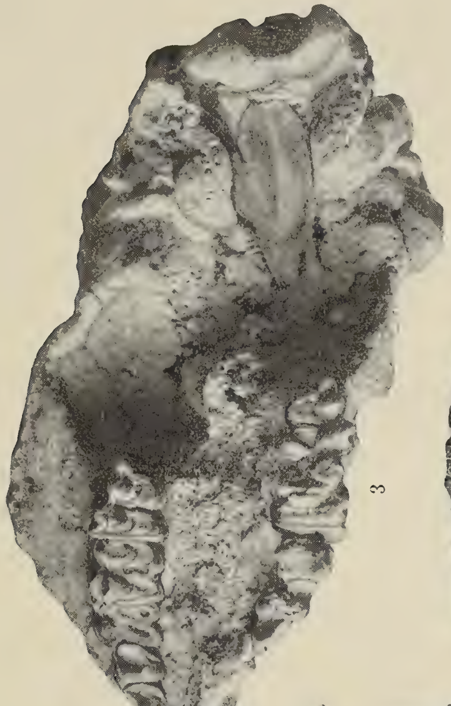
FIG. 1—Crushed skull, type specimen, No. 1721. View shows side and top of skull; x 3/4.

(?) *Bothriodon* cf. *brachyrhynchus* (Osborn and Wortman)

FIG. 2—Dp$\underline{3}$ and Dp$\underline{4}$, No. 1722, occlusal view; x 1 1/2.

Hypertragulus fontanus n. sp.

FIG. 3—Skull and dentition, type specimen, No. 473, ventral view; x 1 1/2.
FIGS. 4, *4a*—Right ramus of mandible, No. 1723, lateral and occlusal views; x 1 1/2.
Calif. Inst. Tech. Coll. Vert. Pale. Sespe Oligocene, Las Posas Hills, California.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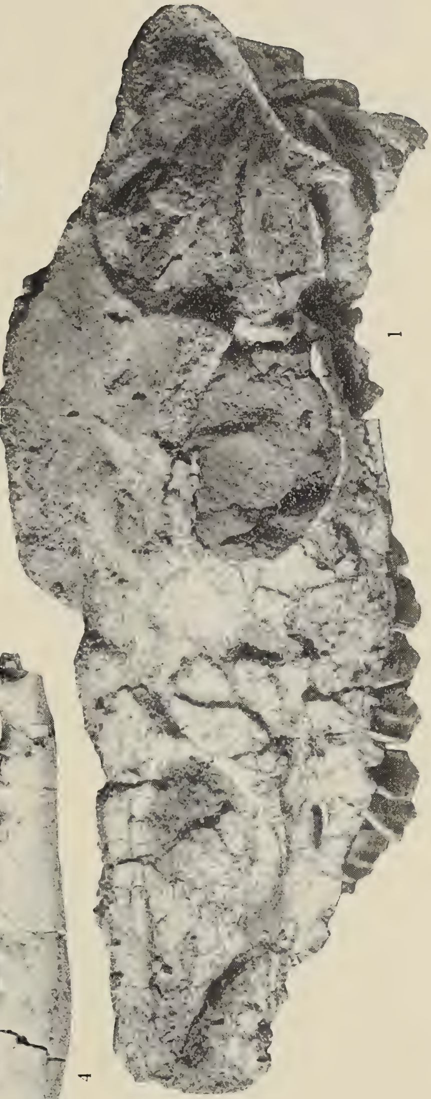
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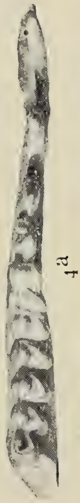
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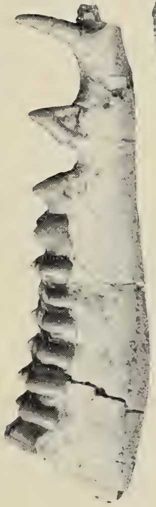
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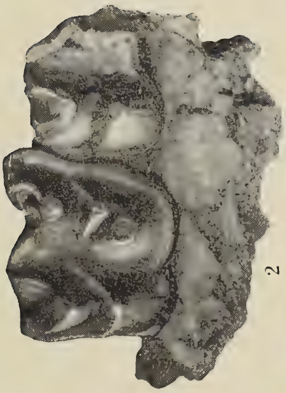
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